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OF THE

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STUDIES IN THE KUHNIIINAE (EUPATORIEAE) II *

L. O. GAISER

With five plates

INTRODUCTION

Liatris and *Brickellia*, the two largest genera of a small subtribe of the *Eupatorieae*, which Robinson (1913) called the *Kuhniiinae*, were examined cytologically and found to have the basic chromosome numbers of 10 and 9 respectively. *Brickellia* with approximately ninety species (Robinson 1917) has its greatest distribution in Mexico and southwestern United States. It extends northward to the Canadian border and southward into Central America and sparingly into Brazil. The range of *Liatris*, with thirty-two species (Gaiser 1946), is confined almost entirely to southern Canada and the United States, though it just crosses the border into Mexico. The remaining seven genera are small. However, their distribution in the American hemisphere is interesting in relation to the two large genera mentioned. *Barroetia* is wholly Mexican and *Kaninia* is found only in South America. Two others, *Trilisa* and *Carphephorus* occur only in southeastern United States while the monotypic genus *Garberia* is limited to Florida. Only the two genera, *Kuhnia* and *Carpochaete* overlap from United States into Mexico.

The comparative growth-form of these genera is also a matter of interest. *Liatris* is a genus of perennial herbs with mostly corm-like rootstocks, though in the series *Punctatae*, deeply penetrating roots occur, and the singular *L. Garberi* of the *Spicatae*, has a tuberous form. By contrast, *Brickellia* consists largely of shrubs or shrubby perennials, of which probably the most woody is *B. argyrolepis*, which attains a height of twelve feet and a stem diameter of two inches (Gaiser 1953). It is difficult to sharply differentiate between herbs and shrubs in this genus, for the stem is often only slightly woody at the base or consists of a woody caudex. Others are perennial herbs with only persistent underground parts which are fusiform, tuberous or more knobby and rhizomatous. Only one species, or possibly two, are annuals. Of the seven species of *Barroetia* (Robinson

*Chromosome Studies in the Kuhniiinae (Eupatorieae). I. *Brickellia*. *Rhodora* 55: 253-267, 269-288, 297-321, 328-345 (1953).

1911b), one is known to be a perennial herb, somewhat woody at the base, and three are recognized as annuals. *Kuhnia* species are comparatively slender herbs with long somewhat conical roots which have been described by Shinnars (1946) as irregularly divided at the top and becoming more or less "soft-woody." Robinson (1911a) described *K. adenolepis* as having a woody caudex. *Carphephorus* and *Trilisa* are true perennial herbs having clustered, thick, almost tuberous roots and leafy rosettes. The single species of *Garberia* is definitely a woody shrub attaining a height of six to eight feet, while the species of *Carpochaete* are generally spoken of as small branching shrubs.

In the cytological studies of *Liatris*, including all the given species except *L. lancifolia*, only the diploid number ($2n = 20$) was found in those of nine series, while polyploidy prevailed in the *Punctatae* (Gaiser 1949, 1950, 1951). In one species only the hexaploid number was found, in a second, only the tetraploid, in a third, the diploid, while both diploid and tetraploid numbers occurred in two others. Further, one of these two latter, *L. punctata* Hook. has the widest distribution of any species in the genus, extending the full north-south range from western Canada, east of the Rocky Mountains, over the Mexican border. In forty-one species of *Brickellia* examined, representing half of the undoubtedly distinct species, and four sections, only the diploid number ($2n = 18$) was found.

On the basis of previous cytological work, it seemed worth while to determine¹ the chromosome numbers in the other genera of this small group of the *Compositae* with the hope that new clues of relationship would become evident. From fossil evidence, the family is believed to be of recent development. With the two largest genera known to differ by one in their chromosome number, questions arose: Was there a smaller basic number? If so would it be found in genera limited to the tropics or to the more woody forms? Would those that were shrubby have the same number as *Brickellia* and the perennial herbs the same as *Liatris*? Or would there be still further variations in number and if so what relationship would this bear to the classification?

There was also the interesting problem of polyploidy, since though lacking in *Brickellia*, it was found in *Liatris*, a genus limited to the temperate zone. There have been contributions which fail to confirm but also some which give support to Hägerup's original hypothesis (1932) that polyploidy developed under rigorous environmental conditions. In Stebbins' (1950) discussion on the topic of the polyploid complex and geographic distribution he stated that no tropical group was known well enough to be included. When undertaking the study of *Brickellia*, it was expected that because of its range into Mexico and Central America it

¹The author gratefully acknowledges a grant from the Canadian Research Council when a beginning was made. Subsequently the project was assisted by a grant from the American Philosophical Society which permitted the collection of species of *Barroetia* and *Kuhnia* as well as *Brickellia* in Mexico, without which this investigation could not have been completed.

would include tropical forms. Field experience in the collection of approximately two dozen species from Mexico and Guatemala impressed upon the author that they were on the plateaus and thus were actually existing in a temperate climate. The annual *B. diffusa* is somewhat exceptional for although it occurs on the plateaus too, it is the only species to be found throughout the Caribbean. All of the species of *Barroetia*, according to Robinson (l.c.) occur on the plateaus in Mexico, and no species has penetrated northward beyond its central zone. There is no monograph of *Kanimia* but the labels on specimens at the Gray Herbarium indicate that they have come from regions in the Andes from the Colombian border to Peru and the province of Minas Gerais, Brazil. Thus there are not included in this subtribe, plants of tropical lowlands such as make up the genus *Anthurium* of the *Araceae*. But we know that polyploidy does appear in five of a total of thirty-nine species of that genus examined (Gaiser 1927). Stebbins (1950) apparently overlooked this when he made the statement cited above. In contrast to one large tropical genus, as *Anthurium*, the *Kuhniinae* present a challenging succession of related forms which appear to have progressed northward from the tropics in varying degrees.

NOTES ON THE TAXONOMY OF THE GENERA

In his key to the *Eupatorieae*, Robinson (1913) added an additional subtribe to those given by Hoffmann (1890), and changed the name of the *Adenostylinae* to *Kuhniinae* because the assumed type genus *Adenostyles* did not really belong to the tribe. With its omission from this subtribe, the other nine genera remain the same.

Of them the genus *Kanimia* stands alone in having a definite number of phyllaries. Both in the number of florets and phyllaries it is like *Mikania*, from which Hoffmann (l.c.) had stated it was only separated by its 8–10 ribbed achene. However, *Mikania* is placed at the end of the previous subtribe *Ageratinae*. There is no general treatment of *Kanimia*. Thirteen species have been described from Colombia, Peru, Ecuador, and Brazil. Because it is South American, consists largely of vines or woody forms, as are included in the much larger genus *Mikania* and has a definite number of florets and phyllaries, a strong link is suggested between the two subtribes. Whether the chromosome number would be of any help in adjustment of generic segregation, will have to await the procuring of cytological materials of *Kanimia*.

It is a matter of great satisfaction that of the remainder, the four largest genera had been monographed, and two of them by Robinson, whose specialty was the *Eupatorieae*. Thus we have the excellent treatment of *Brickellia* in 1917, following that of *Barroetia* in 1911, and the key to the whole group in 1913. The genus *Kuhnia* was dealt with by Shinnars in 1946, as had been one series of the genus *Liatris*, the *Scariosae*, in 1943. The latter genus was in the process of being revised by Gaiser at that time and publication followed in 1946. Of the four other genera still

lacking comprehensive treatments, a brief summation of their status is given here.

Carphochaete

Next to the singular *Kanimia*, *Carphochaete* stands apart from the rest of these genera in the nature of its pappus, which is scale-like and dilated at the base, instead of being setose.

There has been no recent treatment of this genus, which was established by Gray (Pl. Fendl. 65, 1849). It was based on a somewhat shrubby herb from northern Mexico, and named *C. Wislizeni* for its collector. In 1852, Gray (Pl. Wright. 89) emended the description of the genus as shrubby or herbaceous but shrubby at the base, when describing two new species, one Mexican, *C. Grahamei*, and the other from the boundary region of Mexico and New Mexico, *C. Bigelovii*. Since then only one other species has been added by Greenman (Proc. Am. Acad. Arts & Sci. 44: 34, 1904). It also is Mexican and was considered as an herbaceous perennial having a ligneous base. As the author's description has distinguished it from the other Mexican species, chiefly by the leaves and phyllaries, it is clear that all four species are similar in their shrubby or near shrubby nature. It was possible to include the American species in this study.

Garberia

Another shrub of this subtribe is found in the genus *Garberia*. When cataloguing a collection of plants that had come from east Florida, Nuttall (Amer. Jour. Sci. 5: 299, 1822) gave a brief Latin description of *Liatris fruticosa*. It was the only species of that genus referred to as fruticose by DeCandolle (Prod. 5: 132, 1836) and became the subdivision *Suffruticose* in Torrey and Gray (Fl. N. Am. 2: 76, 1841). This plant, referred to by Nuttall in 1841 (Trans. Amer. Phil. Soc., ser. 3, 7: 285) as agreeing with the genus *Liatris* in its flowers but not in its habit, was transferred by Gray (Proc. Acad. Nat. Sci. 379, 1879) to the new genus *Garberia*. Thus it appears in more recent floras of the South as *Garberia fruticosa* (Nutt.) Gray. The restudy of William Bartram's plants (Bartr. Trav. 164, 1791; ed. 2 162, 1792) by Merrill (Bartonia 23: 24, 1944) called for a new combination. After Dr. Francis Harper had covered Bartram's routes, he was satisfied that what Bartram had described as *Cacalia heterophylla* was the same shrub. The plant is now known as *Garberia heterophylla* (Bartr.) Merrill & F. Harper. It still is the only representative of the genus.

Carphephorus

The genus *Carphephorus* was established by Cassini (Bull. Soc. Philom. Paris p. 198, Dec., 1816) when naming as *C. pseudo-liatris*, a specimen without locality, seen in the Jussieu herbarium, which for a time was thought to be of Siberian origin. In his Dictionnaire, Cassini (Dict. Nat. Sci. 7: 148, 1817) explained that it belonged to the natural Tribe *Eupatorieae*, "section des *Liatridees*," in which he was placing it, near *Liatris*, the chaffy receptacle being the chief point of difference. Cassini's "sec-

tional" name must be rejected because under the international code a section is of infra generic rank, while Cassini applied this term to a group of genera. Torrey and Gray (1841) found that the character of the receptacle had been overlooked by some in describing other species and rightly recognized *Carphephorus* as an American genus. At that time, three other species were transferred from the genus *Liatris*, *L. bellidifolia* and *L. tomentosa* (Michx. Fl. Bor. 20: 93, 1903) and *L. corymbosa* (Nutt. Gen. 2: 132, 1818). At the same time also the older synonyms were given for these four species, as they were given by Gray (Syn. Fl. 1(2): 1886); hence they have not been repeated here. They still remain the four accepted species of the genus and all have been represented in this study.

Two Californian plants described as *Carphephorus junceus* Benth. (Bot. Sulph. 21, 1844) and *C. atriplicifolia* Gray (Proc. Am. Acad. Arts & Sci. 5: 1591, 1861) were early placed in the *Helanthoideae* instead of the *Eupatorieae*, and assigned to a new genus *Bebbia* by Greene (Bull. Cal. Acad. Sci. 1: 179, 1885). Thus though appearing under the genus *Carphephorus* on page 113 in Gray (Syn. Fl. 1(2) 1886), they are given under *Bebbia* in the supplement of that volume (p. 453). More recently, *B. atriplicifolia* (Gray) Greene has been reduced to varietal rank by I. M. Johnston (Proc. Cal. Acad. Sci., ser. 4, 12: 1197, 1924) so that this genus includes one species, *B. juncea* (Benth.) Greene, its variety *atriplicifolia* (Gray) Johnston, and variety *aspera* Greene (l.c.), all removed from *Carphephorus*.

Other excluded names and species are:

Carphephorus baicalensis Adams in Mem. Soc. Nat. Moscou 5: 115 (1817); DC. Prod. 5: 132 (1836) = *Saussurea pycnocephala* Ledeb. according to Benth. & Hook., Gen. Pl. 2: 249 (1873).

Carphephorus cordifolius DC. Prod. 7: 267 (1838) = *Brickellia cordifolia* Robinson, Proc. Am. Acad. Arts & Sci. 47: 200 (1911).

Carphephorus revolutifolius DC. Prod. 5: 132 (1836) according to Benth. & Hook. Gen. Pl. 2: 249 (1873) "certainly from description, expelled from the genus."

Carphephorus triangularis (DC.) Gray Pl. Wright. 1: 86 (1852), ex Hemsl. Biol. Cent. Am. Bot. 2: 109 (1881); *Bulbostylis triangularis* DC. Prod. 7: 268 (1838) = *Eupatorium vitifolium* (Sch. Bip.) Robinson, Proc. Am. Acad. Arts & Sci. 51: 537-8 (1917), *Hebeclinium vitifolium* Sch. Bip. ex Klatt Leopoldina 20: 90 (1884).

Trilisa

For the genus *Trilisa*, which Cassini (Bull. Soc. Philom. Paris, p. 140, Sep., 1818) established two years after the genus *Carphephorus*, the type was *Liatris odoratissima* Willd. (Sp. Pl. 3: 1637, 1803). Willdenow had taken up this name from Walter's *Anonymos odoratissimus* Walt. (Flor. Carol. 198, 1788), as he had also *A. paniculatus*, these names being declared illegitimate by article 33 of the International Code of Botanical Nomenclature. In his key of the *Eupatorieae*, Cassini (Dict. Sci. Nat. 26: 228, 234, 1823) placed this new genus in his section "*Liatridees*" between *Carphephorus* and *Suprago*, a name which has been retained for the plu-

mose section of *Liatris*. However, Cassini's genus was not accepted at once. DeCandolle (Prod. 5: 131, 1836) used it as a sectional name of the genus *Liatris*, and this was followed by Torrey and Gray (Fl. N. Am. 2: 76, 1841). The latter, however, correctly eliminated unrelated species and limited it to these two, collecting their older flora- and plate-references not included here. Since Bentham and Hooker (Gen. Pl. 2: 248, 1873) referred to the incorrect use of Cassini's generic name for a section, there has been no further confusion of this small genus.

One further species has been added. Small (Bull. Torr. Bot. Club 51: 392, 1924) had described a new plant from Florida under a generic name, an anagram of *Trilisa* which it resembled somewhat in habit, as *Litrisa carnosa*. When Robinson (Contrib. Gray Herb. new ser., 6: 104, p. 49, 1934) closely compared the plant with *Trilisa* and *Carphephorus*, he was led to refer it to the former genus.

MATERIALS AND METHODS

The same methods have been employed as were used in the study of *Brickellia* (Gaiser, l.c.). As some of these materials were collected along with those of *Brickellia*, frequently preparations of both were carried along together so that there might be as little variation in treatment as possible. Whenever seeds were received on herbarium specimens or in packets from other collectors,² they were germinated and eventually treated by the same variety of techniques and stains. In the preparation of figures of the chromosomes, the same photographic and microscopic equipment has been used at the same magnification, with the intention of making adequate comparisons of the size and morphology of the chromosomes with those of *Brickellia*. Thus not only the same terms are used, but with the same connotation of size. The same precautions were taken to study a sufficient number of cells so as to be able to choose similar stages for comparison of the chromosomes of all species of the different genera. Usually comparable stages of each have been photographed, but where the illustrations represent slight variations of condensation, the purpose of the selection has been discussed. In this study, use has been made of the photographic lens to illustrate the trichomes and epidermal figures, both to elucidate and confirm the drawings used for *Brickellia*.

In Table I are given the list of accessions of each species received along with the place and date of collection and the collector's name and number.³ They have been arranged and discussed in the order of a key prepared for the genera (see page 124). As it has been impossible so far to obtain seeds or any cytological material of even a single species of *Kanimia* from South America, that genus is not included in this key.

Following the pattern of the investigation made of *Brickellia*, leaves of the species of these genera were similarly cleared for the study of trichomes.

² The author again expresses deep gratitude to all contributors.

³ Reference to the numbers of collectors will permit examination of a number of specimens in various herbaria. Specimens collected or received by the author will be deposited in the Gray Herbarium.

As stated there, presence or absence of trichomes was not considered important for these studies. Attention was given to their form, as that has been found to change little, if at all, under varying environmental conditions. The terms applied in the descriptions and figures 61 to 88 of *Brickellia*, have again been used here. The same principle was adopted of obtaining leaves at the Gray Herbarium of specimens which had been referred to by authors so that they would approach the typical. As these genera are comparatively small, it was possible to examine one to several leaves of almost all the species and their varieties. It must be pointed out that it does not represent an examination of leaves of numbers of specimens of any species. The difference in upper- and lower-most cauline leaves were illustrated for one species, *Trilisa paniculata*. Changes in the ontogeny of the species were not generally studied in detail.

OBSERVATIONS

I. Seedling growth

Whenever possible, an effort was made to grow some of the germinating seeds for a time at least, in the greenhouse. Attempts to bring the plants into bloom met with varying success. Of three species of *Carphephorus*, two of *Trilisa* and the one *Garberia* none ever produced flowering axes under the same conditions which stimulated flowering of more than a dozen species of *Brickellia*, three species of *Kuhnia*, two of *Barroetia* and one of *Carphochaete*. At least several plants of *Trilisa paniculata* were kept for more than three years, a period longer than normally would be required for a biennial plant to come into flower, and above ground they still had only rosettes of leaves. Time and facilities did not permit further studies along this line.

The plantings attracted attention because of the striking differences of the seedling conditions. As has been described and illustrated for eighteen species of *Liatris* (Gaiser 1950a), during the first season, while the primary root is becoming very much thickened, those seedlings produce only radical leaves. As can be seen in figures 42 to 62, the larger ones with a longer growing period, have formed quite a rosette. Then in the second season, usually a flowering spike is produced. This was also illustrated in the progeny of a natural hybrid (Plate II c, Gaiser 1951). Young plants of *Liatris punctata* were here compared with those of the other genera.

In figures B and C are shown seedlings of *Carphephorus pseudo-liatris* II and *Trilisa paniculata* VIII, of approximately sixteen and eighteen months respectively, in comparison with one of *Liatris punctata* (Fig. A) of approximately two years. The latter is old enough to show the beginning of a forking and the subsequent elongation into the deeply penetrating system which is characteristic of this species. In the *Trilisa*, the modification to the thickened somewhat tuberous roots is already evident and to a lesser extent in the younger *Carphephorus* also. At maturity, a similar thickened fibrous condition would develop, for that is common to all the species of the genus. This photograph happens to illustrate the aptness

TABLE I
Chromosome Numbers in the *Kuhniinae*

Name	Growth Form	No.	Accession			Chromosome Number	
			County	Locality of Collection	Collector, No. & Date	n	2n
<i>Carpochaete Bigelovii</i>	Shrub	II	Pima Co., Ariz.	Santa Catalina Mts.	K. F. Parker 7274, 4/29/50		22
<i>Garberia heterophylla</i>	Shrub	IV	Volusia Co., Fla.	North of Ormond	Mrs. H. Butts, Dec., 1947		20
		V	Highlands Co., Fla.	e. of Sebring, Arbuckle Creek	R. Garrett 11/21/48		20
		VI	Flagler Co., Fla.	Korona	R. B. Miller, 2/16/50		20
		VII	Marion Co., Fla.	Ocala Natl. Forest, near Eureka	Miss L. E. Arnold 2/2/50		20
<i>Carphephorus pseudo-liaris</i>	Perennial herb	VIII	Putnam Co., Fla.	10 mis. s.e. of Interlachen	W. B. Fox, 11/18/51		20
		I	Liberty Co., Fla.	3 mis. e. of Hosford on Hwy. #20	H. Kurz, 11/5/49		20
		II	St. Tammany Parish, La.	1 mi. from Slidell on LaCombe Rd.	L. Ewan 19236, 11/25/49		20
<i>C. bellidifolius</i>	Perennial herb	II	Wake Co., N. C.	2 mis. s. of Fuquay Springs on U.S. #15 A	R. K. Godfrey & W. B. Fox 48679, 10/16/48		20

<i>C. tomentosus</i>	Perennial herb	I	Pender Co., N. C.	10 mis. s. of Harrell's store	R. K. Godfrey 12/22/51	20
<i>C. corymbosus</i>	Perennial herb	I	Alachua Co., Fla.	Gainesville	Miss L. E. Arnold 11/19/46	20
		V	Putnam Co., Fla.	10 mis. s.e. of Interlachen	W. B. Fox, 11/18/51	20
<i>Trilisa paniculata</i>	Perennial herb	II	Volusia Co., Fla.	n. of Ormond	Mrs. H. Butts Dec, 1947	20
		VIII	Leon Co., Fla.	23 mis. w. of Tallahassee	H. Kurz 11/5/49	20
		IX	Leon Co., Fla.	23 mis. w. of Tallahassee	H. Kurz 11/5/49	20
<i>T. odoratissima</i>	Perennial herb	I	Alachua Co., Fla.	Gainesville	Miss L. E. Arnold 11/19/46	20
		IV	Highlands Co., Fla.	Along Jackson Creek, near Sebring	R. Garrett 11/10/48	20
		V	Leon Co., Fla.	23 mis. w. of Tallahassee	H. Kurz 11/5/49	20
		VI	St. Tammany Parish, La.	1 mi. w. of Slidell	L. Ewan 1937 11/25/49	20
<i>T. carnosa</i>	Perennial herb	III	Highlands Co., Fla.	w. of Sebring	R. Garrett 11/11/48	20
		IV	Highlands Co., Fla.	wet pinelands s. of Sebring	R. Garrett 11/4/49	20

TABLE I — continued
Chromosome Numbers in the *Kuhninae*

Name	Growth Form	Accession				Chromosome Number	
		No.	County	Locality of Collection	Collector, No. & Date	n	2n
<i>K. eupatorioides</i> var. <i>pyramidalis</i>	Perennial herb	I	Kalamazoo Co., Mich.	Sect. 20, Schoolcraft Twp.	C. R. Hanes 9/17/47		18
		II	Clark Co., Ky.	12 mis. e. of Winchester	F. T. McFarland 10/18/47		18
		III	Brazos Co., Texas	5 mis. s. of College Station	H. B. Parks 10/20/47		18
		VII	Kalamazoo Co., Mich.	Along L.S.M.S. Rwy., Schoolcraft Twp.	C. R. Hanes 1648 10/5/48		18
<i>K. eupatorioides</i> var. <i>texana</i>	Perennial herb	I	Dallas Co., Texas	3100 Block on Rosedale St., University Park, Dallas	L. H. Shinnery 11/11/48	9	18
<i>K. eupatorioides</i> var. <i>corymbulosa</i>	Perennial herb	I	Roosevelt Co., Mont.	10 mis. n.e. of Poplar	M. Ownbey 3229 8/30/49		18
<i>K. Moseri</i>	Perennial herb	I	Alachua Co., Fla.	Gainesville	R. Garrett 11/3/48	9	18
<i>K. rosmarinifolia</i>	Perennial herb	III	Santa Cruz Co., Ariz.	Shaded canyon, Patagonia	D. H. Darrow & Haskell 2317 10/14/44	9	18
		V	Apache Co., Ariz.	Near cultivated land, St. John's	K. F. Parker 7409 12/3/50		18

<i>K. Schaffneri</i>	Perennial herb	I	Mexico, Mex.	Hills of El Salto, n.w. of Huchuetoca	D. B. Gold & F. Matuda 10/30/51	18
<i>Burroetia subuligera</i> var. <i>latisquama</i>	Perennial herb	I	Jalisco, Mex.	Along rocky cut near top of barranca, Guadalaajara	L. O. Gaiser 66 10/27/50	9 18
<i>B. sessilifolia</i>	Annual	I	Puebla, Mex.	Along dry slopes of Cerro Tlacoctli 6 kms. s. of Izucar de Matamoros	L. O. Gaiser 75 10/31/50	9 18
		II	Morelos, Mex.	From the limestone mt. at Yauatepec	L. O. Gaiser 76 11/3/50	18
		III	Morelos, Mex.	ca. 23 kms. from Cuernavaca on mt. slopes on road to Yauatepec	L. O. Gaiser 77 11/3/50	9 18
		IV	Guerrero, Mex.	5 kms. from Taxco, along Mexico to Taxco Hwy.	L. O. Gaiser 88 11/4/50	18

Chromosome Numbers in the Subtribe *Ageratinae*

<i>Mikania scandens</i>	Vine	II	Calvert Co., Maryland	Plum Point	S. F. Blake Autumn 1946	38
		III	Flagler Co., Fla.	Haw Creek Region	Mrs. H. Butts Autumn, 1946	38
		VII	Highlands Co., Fla.	Rich wet soil, Sebring	R. Garrett 11/15/48	38
<i>M. cordifolia</i>	Vine	I	Highlands Co., Fla.	Highlands Hammock, State Park	R. Garrett 11/23/48	38



SEEDLINGS

of the specific name *pseudo-liatris*, given by Cassini to his type species of the genus. While narrower, linear leaves are found in a number of species of *Liatris* other than *L. punctata*, this is the only species of *Carphephorus* possessing them. It is obvious that regardless of the shape and the structure of the root, development of a rosette of leaves is common to all and is of rather prolonged duration. At least under greenhouse conditions, this same *Trilisa* seedling has not varied much in appearance in more than three years.

Figures D to G represent comparatively much younger seedlings of *Carpchoacte Bigelovii* II, *Barroetea sessilifolia* I, *Kuhnia rosmarinifolia* V and *Brickellia adenocarpa* III. Only records were kept of the time of sowing the seeds, so that from those dates, the *Carpchoacte* is a little more than a month old, the *Barroetea* is less than three months, the *Kuhnia* a little more than two months and the *Brickellia* less than two months. All have developed slender fibrous roots at this time but already show a fast growing stem-axis with a number of nodes and internodes. This similarity in seedlings cannot be attributed to any likenesses of their actual growth-form, for while this species of *Barroetea* is an annual and might be expected to show very rapid growth, that of the *Kuhnia* is an herbaceous perennial, that of the *Brickellia* a shrubby perennial, and the *Carpchoacte* a small shrub.

The matter of chief interest was that there were two types into which all of these seedlings can be classified: the rosette and the non-rosette.

II. Chromosome Number and Morphology

CARPHOCHAETE

Cells of *Carpchoacte Bigelovii* II were found to have a noticeably greater amount of chromatin than any of the other genera studied. This is due first of all to a larger number of chromosomes ($2n = 22$) but also to the presence among them of a majority of larger ones. While the exact size and form of all the chromosomes is not evident in figure 30, among the thirteen peripherally arranged units can be distinguished some of the long and medium classes.⁴ The V approximately at the center top and the one almost at the center bottom, are designated medium in length (Mm), in contrast to the two long V's along the right (Lm), all of these being medianly constricted. The latter two in turn are distinguished from

⁴The same abbreviations as have been used in Gaiser (1953) are here applied: Using capital letters to express length, long chromosomes with median, submedian and subterminal constrictions are represented as Lm, Lsm, and Lst respectively, chromosomes of median length similarly constricted as Mm, Msm and Mst, and short chromosomes similarly Sm, Ssm and Sst. The short short class became SS; when medianly constricted SSm and when terminally SSt.

EXPLANATION OF FIGURES OF SEEDLINGS

Figures represent seedlings of various accessions of different dates. Figs. A-C photographed 5/9/51. Figs. D-G photographed 4/26/51.

A. *Liatris punctata* 11/22/49. B. *Carphephorus pseudo-liatris* II 1/19/50. C. *Trilisa paniculata* VIII 11/22/49. D. *Carpchoacte Bigelovii* II 3/20/51. E. *Barroetea sessilifolia* I 2/26/51. F. *Kuhnia rosmarinifolia* V 2/15/51. G. *Brickellia adenocarpa* III 3/5/51.

two of similar length but having submedian constriction (Lsm), at right and left at the top, and a pair along the left side, in slightly lower focus, which are subterminally constricted (Lst). With the remaining marginal V at the lower left clearly a long chromosome also (Lm), a total of seven of the long class have been counted merely among the peripheral ones. As frequently occurred, toward the center among others, are six shorter units (Sm) of which two can be distinguished at lower left. In a similar cell (Fig. 29) of a Feulgen preparation, only one medium chromosome was left with these six, all of which are short V's and medianly constricted, to fill the center around which fifteen long and medium ones were arranged marginally. There is a sharper break between the six short ones and the remaining sixteen than separates the equal number of long and medium ones into which that number has been divided. In the short ones there was little doubt that the constriction was median. The eight long chromosomes were analyzed as to centromere position with less difficulty, than those of medium length where there was some uncertainty. From the study of material available of one accession the karyotype has been given in Table II as: 2 Lm, 4 Lsm, 2 Lst, 4 Mm, 2 Msm, 2 Mst and 6 Sm.

GARBERIA HETEROPHYLLA

This monotypic species, restricted to Florida, was received through five different collectors from as many different counties. Excellent material was available for study and no variation was found. In a cell (Fig. 28) of accession VI from Flagler County, the number of chromosomes can be counted ($2n = 20$) and their morphology is also clearly recognizable. Thus, by beginning as at twelve, and proceeding clockwise around the dial, the marginal chromosomes represented in succession are as follows: Mst, Lst, Sst, Lsm, Mm, Msm, Lm, Lsm, and Sm. In the cell there are a pair of each of these classes except Mm, and of that there are three pairs. A second cell (Fig. 27) in the same section, shows that two of the shortest units, lower left and right margins, are heterobrachial. This was more convincing in cells particularly favorable for study of accession VII, though not photographed to much better advantage (Fig. 26, 3rd from left at top). By comparison with the cells of *Carphochaete* there is this difference of the fewer (four rather than six) chromosomes of the short class, and in their variation from the uniformly similar isobrachial type. As for the rest, the same classes are present though not to the same numbers. With one pair of long of each of the three constriction types, rather than a total of eight long ones, comes a further reduction in amount of chromatin. This karyotype has the greatest variety: 2 Lm, 2 Lsm, 2 Lst, 6 Mm, 2 Msm, 2 Mst, 2 SM, and 2 Sst.

CARPHEPHORUS

Two of the four species of *Carphephorus* were examined from at least two accessions, while *C. tomentosus* and *C. bellidifolius* were limited to one each. In all, the $2n$ chromosome number was found to be 20.

Of *C. bellidifolius* there were a number of excellent cells for study.

From comparisons made with *Carphochaete Bigelovii* it was observed that the chromosomes were all more nearly equal in length. Two pairs of medium chromosomes one each with medium, Mm, and submedian, Msm, constrictions, were almost as long as the long chromosomes. Also the next to the shortest pair were not sharply different from the medium in length. Frequently when the karyotype was assembled after an analysis of a cell, there were odd numbers for these two classes. The slightly more condensed chromosomes of figure 22 were well spread. Beginning as at seven and proceeding clockwise to four, the marginal ones are: Mst, Mm, Mm, Lst (pale, as slightly below focus), Lsm, Mm, Mm, Mst, Lst, Lm, Msm, and Msm. The two latter and the pair, Mm, directly opposite, closely approach the long ones. In this cell the shortest units are toward the center.

Preparations from seeds of *Carphephorus tomentosus*, which had been received from North Carolina, were more adequate for study than photography. As in the cell of figure 23, the chromosomes may be spatially separated but slight overlapping of the ends confuses the picture. Under the studies of this species the note had been made "remarkably few short chromosomes."

As was customary accompanying the studies of cells, diagrams of *C. corymbosus* V were made and the pairs of chromosomes numbered in succession as to their lengths. With a total of twenty chromosomes, the numbers of the shortest pairs were 9 and 10. While the latter was sure to be of the class Sm, opposite 9 there was frequently placed the question, "short or medium." In figure 24 for example, along the right side two isobrachial chromosomes which are clearly medium in length, alternate with two which are heterobrachial. These latter were numbered 9 and 8 respectively, meaning that while the bottom one was one of the characteristic medium pair with subterminal constriction, Mst, the second from the top was of the questionable class.

Accessions of *C. pseudo-liatris* from Florida and Louisiana were compared. Because tips were available from seedlings (see Fig. B) growing in a pot, as well as from germinating seeds, the most convincing analysis of the morphology of the chromosomes was made of this species. In figure 25, photographed when one each of the two shortest pairs are in focus, a number of the longer chromosomes are foreshortened. Almost at center bottom is a short medianly constricted chromosome, Sm, while the second from the center top is heterobrachial. Frequent analyses left a question concerning the members of this pair, just as had been the case in studies of the other species. Certainly no marked difference was noted for any one. Therefore one karyotype has been given for the four of them: 2 Lm, 2 Lsm, 2 Lst, 6 Mm, 2 Msm, 4 Mst, and 2 Sm. This modification of the two last classes was made with hesitation but allowing for the factor of human error, was accepted on the evidence of the camera.

TRILISA

Of several collections of *Trilisa paniculata*, made in South Carolina in October, germination of seeds was very poor, though it was possible to



CHROMOSOMES
(Caption at bottom of facing page)

obtain the chromosome count, $2n = 20$. More somatic divisions were obtained from two accessions from northern Florida in November and a few seedlings were grown (see Fig. C). While a majority of longer chromosomes in a peripheral arrangement was the more usual, in figure 19 some of the medium and short units are seen in this position. Thus a better idea of the comparative lengths of all the classes of units for this species is obtained. At the top left corner, two medium chromosomes, the one subterminally, Mst. and the other medianly, Mm, constricted, lie respectively below and above a long submedian one. The mate for the former appears at the opposite right hand corner between two radiating long chromosomes of subterminal constriction, Lst. Below these, one each of the longest and shortest medianly constricted chromosomes are sharply contrasted and followed by a similar one medium in length. The latter is one of the medium class which approaches the long. Certainly this medium chromosome and the long one are more nearly equal than it and the short one. In size and form no noticeable variation from the chromosomes of the species of *Carphephorus* was evident. Comparison of this cell with figure 24 of *C. corymbosus* brings the camera's confirmation. The same question arose as to the length of the pair next to the shortest, but they were considered to be heterobrachial and not unlike the class Mst.

Preparations were made from seeds of *Trilisa odoratissima*, known as the Vanilla Plant, from Florida and Louisiana. The long chromosomes were more prevalent and of the same form as in the previous species. Also, there was no evidence that the medium and short ones differed. Because of the abundance of cytoplasmic inclusions in the cells of this species, fewer cells were suitable for photography. When the chromosomes were well spread, globules were often overlying. It would have been better to have made all preparations by the Feulgen technique. Figure 20 is of a cell just back of the meristematic apex and the chromosomes are therefore more crowded. One karyotype is believed to be common to these two species and it has been found to be indistinguishable from that of *Carphephorus*.

EXPLANATION OF FIGURES

Figs. 1-7, 9-30, are from near comparable metaphase plates in root-tips. Fig. 8 is of an early anaphase plate. 1, 2, 3. *Barroetia sessilifolia* I. 4, 5. *B. subuligera* var. *latisquama* I. 6-10. *Kuhnia eupatorioides* var. *pyramidalis*; 6-8. (III from Texas), 9. (II from Kentucky), 10. (VII from Michigan). 11. *K. eupatorioides* var. *texana* I. 12. *K. eupatorioides* var. *corymbulosa* I. 13. *K. Mosieri* I. 14-16. *K. rosmarinifolia*; 14, 15. (of accession III), 16. of V. 17, 18. *K. Schaffneri* I. 19. *Trilisa paniculata* VIII. 20. *T. odoratissima* IV. 21. *Mikania scandens* III. 22. *Carphephorus bellidifolius* II. 23. *C. tomentosus* I. 24. *C. corymbosus* V. 25. *C. pseudo-liatris* I. 26-28. *Garberia heterophylla*; 26. of accession VII, 27, 28. of VI. 29-30. *Carphochaete Bigelovii* II.

Preparations made of root-tips taken from plants, fixed in Belling's at the same time and stained in toto in Feulgen's, Figs. 5, 11, 12, 25, 29. Root-tips of seeds after Belling's and stained in N.G.V., Figs. 16, 24; after Karpechenko's and stained in Feulgen's, Figs. 9, 18, 27, 28. All the rest were of seeds fixed in Karpechenko's and stained in N.G.V. The photomicrographs were taken with the use of a Zeiss microscope and a Homal IV lens. All figures 2300x. Reduced 1650x in reproduction.

The preparation of the plates has been aided by a grant from The Society of Sigma Xi, which the author gratefully acknowledges. It is a pleasure to acknowledge the assistance of Mr. Paul Brown in the photomicrography.

The rarer species, *Trilisa carnos*a, limited to Florida, which had been thought to merit new generic rank by Small, was received from the same locality near Sebring, three times from October to November, 1948, and again in November, 1949. The difficulty of germinating seeds of this species was certainly not overcome during the time and with the material available. Only a few seeds ever appeared to begin growth and none developed very far so that an extremely limited number of mitoses were found. The number ($2n = 20$) and approximately the same kinds of chromosomes as found in the other two species were sketched from cells not adequate for photography. However, lacking sufficient material for careful studies, the karyotype of this species cannot be included at this time.

KUHNIA

Three of the four American species given by Shinnars (l.c.) have been available for this study. Accessions had been received of the largest, most widely distributed species, *K. eupatorioides* L. from the states of Michigan, Kentucky, Texas and Montana, which, according to Shinnars (l.c.) would represent all the varieties of that species except *ozarkana* Shinnars. Those from the first three sources were variety *pyramidalis* Raf. and from the last, var. *corymbulosa* T. & G. while Dr. Shinnars himself contributed a packet of seeds of his variety *texana*. A glance at figures 6 to 12 of this polymorphic species, shows a chromosome plate of $2n = 18$, in which there are lacking any of the long chromosomes, so characteristic of the genera here previously discussed.

K. EUPATORIOIDES variety *PYRAMIDALIS*. From preparations of particular clarity, stained with Newton Gentian Violet five years ago, the sizes of the chromosomes can be shown. At the lower left in figure 6, a parallel pair of the shortest and longest units, both medianly constricted can be compared with a single chromosome of intermediate length, lying almost horizontally above them. The units of this figure are probably all a little more condensed than those in figure 7, which is of a cell in a similar preparation. In the latter, the two longest chromosomes are at outer left and right and are submedianly constricted. From such figures, it is clear that the longest chromosomes would have to be placed in the medium class, according to the scale of sizes here used. One might then expect the shortest chromosomes, since there are units intermediate in length, to be two classes removed and to fall into a short short class, as adopted for some species of *Brickellia* (Gaiser 1953). Considerable effort was made to decide this question by comparison of various stages and of cells of all the accessions. Figure 8 is of an anaphase plate of a recent mitosis as can be judged by the parts of two chromosomes outlying in the cytoplasm at the right, belonging to the other closely overlying plate. The chromosomes are more slender but again they do not cover three distinct classes of length. It is considered that the karyotype includes medium to short chromosomes, and when there are nine pairs of such closely approximating lengths there is difficulty in deciding the boundary between the two classes.

In figure 8, two chromosomes with very small terminal bodies are seen, one at center bottom and the other at center left. More frequently cells were found in which only one such satellite was visible, as is shown at the end of the curved chromosome at upper right of figure 6 and at the inner end of the chromosome stretching toward the center from the left of figure 7. It is believed these chromosomes are next in length to the two longest pairs. By careful analysis of numerous cells of other accessions as well as this, next in succession of length are: 2 Msm and 2 Mm, which more closely approach the aforementioned three pairs than do the other 4 Mm. Whether the latter should be classed as short may be debatable. The four shortest are considered 2 Sm and 2 Sst. In preparations of accession II from Kentucky (Fig. 9) as well as accession VII from Michigan (Fig. 10) this analysis was also favored.

K. EUPATORIODES variety *TEXANA*. In the second accession from Texas, the figures are very much the same. Cells without any visible satellites were more frequently found than those showing them even delicately as in figure 11 (the second chromosome on the upper left) from a Feulgen preparation.

K. EUPATORIODES variety *CORYMBULOSA*. The western variety was received from Montana. Well spread chromosomes in the plate of such a cell as shown in figure 12 help to confirm the previous analyses. At the center on the left side is the medium chromosome with a satellite appearing knob-like at its inner tip and close to its centrally placed mate. Above them, occur one each of the longest of Msm and Mm respectively. The curved pair at center bottom are the second pair of so-called Msm while the two overlapping as a V at top are second in length of Mm. It is evident from such a preparation that no sharp line separates the classes of chromosomes. However, on the basis of comparison with those of the other genera the karyotype is believed to be: 8 Mm, 4 Msm, 2 M with sat., 2 Sm, 2 Sst.

Of the two other American species of *Kuhnia* included, the first is a restricted endemic in lower Florida. Two cells of *K. Mosieri* Small, in which the chromosomes were well separated by microscopic adjustment, could be seen in the field of the microscope at one time. Starting with the longest chromosomes, successively those next in size were sketched in different colors and the two cells constantly compared. Unfortunately they did not photograph as well as it was possible to draw them, to add to this interesting exercise. Of course there were points of indecision. However, even before it was recognized that in one of these (Fig. 13, center left) a chromosome with a satellite was represented, its arrangement in the order of consecutive chromosome lengths coincided with that given to such in *K. eupatorioides*. The karyotype of these two species were found indistinguishable. The second species is commonly known as *K. rosmarinifolia* Vent. Shinnars (l.c.) considered this name a "nomen confusum" and put it in synonymy with *K. chlorolepis* Wooton & Standley. Blake (1942) did not consider it necessary to adopt this name in his treatment of the genus for Arizona and so I have not, as both accessions

TABLE II
Karyotypes in Species of Genera of *Kuhniinae*

Name	Accessions Studied	Total Number	Chromosomes										Remarks
			Number of pairs each										
			Lm	Lsm	Lst	Mm	Msm	Mst	M with sat.	Sm	Sst		
<i>Carphochaete Bigelovii</i>	II	22	I	2	I	2	I	I	1	...	3		
<i>Garberia heterophylla</i>	IV V VI VII	20	I	I	I	3	I	I	1	...	I	I	
<i>Carphophorus pseudo-liaris</i>	I II	20	I	I	I	3	I	2	...	1	...		
<i>C. bellidifolius</i>	II	20	I	I	I	3	I	2	...	1	...		1 Mst = S ?
<i>C. tomentosus</i>	I	20	I	I	I	3	I	2	...	1	...		
<i>C. corymbosus</i>	IV V	20	I	I	I	3	I	2	...	1	...		
<i>Trilisa paniculata</i>	VIII	20	I	I	I	3	I	2	...	1	...		
<i>T. odoratissima</i>	IV V	20	I	I	I	3	I	2	...	1	...		1 Mst = S ?
<i>Kuhnia eupatorioides</i> var. <i>pyramidalis</i>	I II III VII	18	4	2	...	1	1	1		1 Msm and 1 Mm the longest, other Msm and another Mm next in length.
<i>K. eupatorioides</i> var. <i>texana</i>	I	18	4	2	...	1	1	1		
<i>K. eupatorioides</i> var. <i>corymbulosa</i>	I	18	4	2	...	1	1	1		
<i>K. Mosieri</i>	I	18	4	2	...	1	1	1		
<i>K. rosmarinifolia</i>	III V	18	4	2	...	1	1	1		
<i>K. Schaffneri</i>	I	18	4	2	...	1	1	1		
<i>Barroetia subuligera</i> var. <i>latisquama</i>	I	18	4	2	...	1	1	1		Ditto
<i>B. sessilifolia</i>	I III	18	4	2	...	1	1	1		

here studied came from that state. Of the preparations of *K. rosmarinifolia* III, the same repetition of statements could be made, cells showing a small satellite less frequently seen (Fig. 15, at the center top), than those without them (Fig. 14). Of accession V of this species, a plate of particularly condensed chromosomes was photographed (Fig. 16) to show the narrow gap between the shortest and longest units. Thus, for example, comparison with figures 25 (Gaiser 1953) of *Brickellia microphylla* where the chromosomes were shortened by paradichlorobenzene treatment, or figure 42 of *B. glomerata*, where a similar drastic shortening accidentally happened in one cell of a Feulgen preparation, emphasizes that there is a greater spread in the species of that genus where the karyotype includes long chromosomes.

One of the three species, which do not occur north of Mexico, *K. Schaffneri* Gray, was available for this study. Because the type sheet contains also a root of some legume, Shinnars (l.c.) renamed the species *K. microphylla*, but Blake⁵ considers this unjustifiable.

In a very clear early metaphase plate (Fig. 17) from a Newton Gentian Violet preparation, the range in size of the chromosomes is shown. One of the longest chromosomes, submedianly constricted (Msm) is at the upper right corner and two of the shortest ones, medianly constricted (Sm), can be distinguished as smaller V's among the central group, almost at center top and bottom. At this focus, one arm of several of the marginal V's has been foreshortened. Thus, for example, the chromosome at lower right is the other of the longest pair (Msm) and in succession the other two at center bottom represent medium chromosomes of the next category, Mm and Msm respectively. The straight medium chromosome, which is at a slight angle above the latter, is terminated toward the center by a small knob and is the equivalent of the chromosome with a satellite. The same can be seen in a cell of a Feulgen preparation (Fig. 18) at the tip of the chromosome coming into the small central upper space.

By comparison of figure 17 with that of *K. eupatorioides* var. *corymbulosa* (Fig. 12) of a cell similarly prepared, it might appear that the chromosomes of this species are generally longer, but this is merely so because it is a slightly earlier metaphase stage. It is worthy of note that in both of these cells there is a knob-like body at the end of a pair of the chromosomes. That its appearance cannot be attributed merely to this one kind of preparation is proved by the use of the same kind (e.g., Newton Gentian Violet) in illustrating *K. eupatorioides* var. *pyramidalis* (Figs. 6, 7, 8) and *K. rosmarinifolia* (Fig. 15) where it is seen separated from the chromosome. Yet the same is also visible in Feulgen preparations (see Figs. 11, 18). In summary, in any kind of preparation of all of the species of *Kuhnia* here studied, this very small terminal body, which has been called a satellite, may be found, whereas in similar preparations of the previous genera, no evidences of such has ever been seen. No variation from the

⁵ *In litt.*

karyotype given for *K. eupatorioides* has been found in the three other species studied.

BARROETEA

The one perennial species which is somewhat woody at the base, *B. subuligera* (Schauer) Gray, is known from the northern boundary to Hidalgo, a central state in Mexico. The larger variety *latisquama* Greenman, was described from a specimen collected in Jalisco. A plant of this was collected in the barranca at Guadalajara and from seeds of it, a seedling was grown for a time in the greenhouse. From pollen mother cells as well as root-tips, the chromosome number was found to be the same as in the species of *Kuhnia* studied, $n = 9$ and $2n = 18$.

A comparatively early metaphase of a root-tip cell shows the form of sixteen of the chromosomes, but two short ones which were lying one above the other, resulted in the oval body at the upper right of the figure (Fig. 4). One chromosome of greatest length, submedianly constricted, is seen at lower right and a second in length, medianly constricted, is plainly contrasted at center top with one of the shortest (Sm). By the scale of sizes used for the other genera, neither of the former would exceed the medium class. Thus the karyotype includes medium to short chromosomes only. In this cell a number of the heterobrachial chromosomes are found around the periphery and may appear to be more numerous than in a very comparable stage of a *Kuhnia*, e.g., *Kuhnia Schaffneri* (Fig. 17). However, their number is not greater and in other cells where the chromosomes are a little more condensed (Fig. 5) no confirmation is found of this difference. While no chromosome with a satellite is shown, its equivalent is probably represented in one of medium length, subterminally constricted, for the free terminal body was seen in some other cells.

Of the annual species, *B. sessilifolia* Greenman, seeds were collected from four different localities of three of the central states of Mexico and from root-tips of each, the chromosome number was found to be the same as that of the perennial species, $2n = 18$. It was also possible to grow seedlings (see Fig. E) from two of these accessions and similar meiotic divisions were obtained, $n = 9$.

Figure 1 of *B. sessilifolia* III shows a metaphase stage comparable to that of figure 4 of *B. subuligera* and the sizes of the chromosomes are very similar. On one of the longest chromosomes, at upper left, a satellite is conspicuous. In cells of slightly more condensed chromosomes the same is visible (Figs. 2, 3, lower right). Examination of a number of cells of *B. sessilifolia* I resulted in the same analysis of medium to short chromosomes including one of the former showing a satellite, both in Feulgen and other preparations, either in cells of root-tips taken from the plant or from germinating seeds.

From this study of two species of *Barroetea*, it was found that they were more similar to, than different from, the species of *Kuhnia* seen. The points of likeness consist in having: the same number of chromosomes; chromosomes which range from medium to short across an indefinite

boundary, and, one pair of the medium chromosomes showing a satellite. Certainly no constant difference in the karyotype was detected. It is given as: 8 Mm, 4 Msm, 2 M with satellite, 2 Sm and 2 Sst.

SUMMARY ON CHROMOSOMES

As summarized in Table II.

1. *Carphochaete* is the only genus having 22 chromosomes.
2. All the species of the three genera, *Garberia*, *Carphophorus* and *Trilisa* have 20 chromosomes, in common with a majority of the species of *Liatris*.
3. Four of the seven species studied of *Kuhnia* and two of the species of *Barroetia* have 18 chromosomes, the same number that had been found in all of the examined species of *Brickellia*.
4. Monotypic *Garberia* and the one species studied of *Carphochaete*, are both distinct in their karyotypes. The latter has a greater proportion of long chromosomes with three pairs of isobrachial short chromosomes, while in the former, one of two short pairs are heterobrachial.
5. *Carphophorus* and *Trilisa* could not be distinguished by their karyotypes. Yet they varied from *Garberia* in a closer approach, if not equality, of the shortest heterobrachial pair to the medium class.
6. Long chromosomes are absent in the five species of *Kuhnia* studied, the karyotype consisting of medium to short ones. A pair of medium chromosomes have small satellites.
7. A similar closely graded series of short to medium chromosomes, of which one pair bears satellites, makes up the karyotype in the two species of *Barroetia* studied.

III. Trichomes.

As the type of *B. Pavonii* Gray is in the Boissier Herbarium, only six of the seven species of *Barroetia* could be included in this study of the trichomes of the leaves. Five were found to vary slightly in the abundance of non-glandular trichomes which are uniseriate (Metcalf & Chalk 1950) and of the acuminate type according to the classification of *Brickellia* (Gaiser 1953). The size and the thickness of the wall of the trichome vary very little from species to species. Figure 31 represents that of the annual *B. sessilifolia* and fig. 32, generally a slightly larger form, that of *B. subuligera* var. *latisquama*, the perennial considered somewhat woody at the base. The sixth species *B. glutinosa* Brandegee, with leaves described as densely glandular-puberulent, was found to lack this type of trichome but to have the same biseriate glandular form described as being common to a number of species of *Brickellia*. Along the leaf margin these might be found from a few to seven or eight cells high (Fig. 33). If seen edgewise they appeared as a stipitate somewhat globular organ (Fig. 34). When the flat expanse of the leaf was examined, one saw their apices as two typical hemispherical cells (Fig. 35) or by focussing a little lower as rounded cells above the level of the leaf surface. Figure 36 was taken at

a still lower focus where the epidermal pattern, including a stoma, became evident, but the foreshortened trichome was merely a dark blur. Checking leaves of the other species for this type of trichome, it was found only very occasionally on the underside of the midrib near the petiolar attachment. However, the depressed gland, as used also for *Brickellia* (Gaiser, l.c.), and the punctate condition on the lower surface was common to all except *B. glutinosa* where it was lacking on the lower as well as the upper. As in *Brickellia*, this glandular trichome is a longer stalked condition of the short form arising from the epidermal layer in depressions below what is normally seen as the leaf surface. When a species characteristically develops the elevated form, none or very few, if any, are seen remaining sunken below the leaf surface.

No evidence was seen of the smaller uniseriate capitate glandular trichomes in any species of *Barroetia*.

All the species of *Kuhnia*, according to Shinners' classification, were represented and showed a little more variation in trichomes than those of *Barroetia*. On the upper surface of leaves of *K. adenolepis* they were the shortest, consisting of no more than two or three thick-walled cells, arising from a very heavily cutinized epidermis (Fig. 37). Those of *K. Mosieri* were comparatively short, but consisted of thin-walled cells, almost uniform in diameter, so that the trichome tapered very little (Fig. 38). On *K. Schaffneri* (Fig. 39) a more attenuate trichome, of approximately the same length but with heavier walls, showed a tendency towards the moniliform type of rounded bead-like cells. In all those having thick walls this character was prevalent as shown in the uneven-walled form of the scabroid leaf of *K. rosmarinifolia* (Fig. 40). All the succeeding longer ones have been figured at the same magnification ($220\times$) just as all the shorter ones had, though they were more enlarged ($530\times$). While those of *K. eupatorioides* var. *pyramidalis*, taken from our accession from Kentucky (Fig. 41) resembled that of *K. Mosieri* in the thinner and straight walls, those of varieties *texana*, *ozarkana* and *corymbulosa*, with successively thicker and rougher walls (Figs. 42-44) were attenuate and more moniliform. Those on the scabroid leaves of *K. leptophylla* var. *mexicana* (Fig. 45) and *K. oreithales* (Fig. 46) did not differ much from the latter. In these two species an occasional cell filled with an aggregate crystal was more commonly seen than in any other species. In all of them the apical cell is longer than the rest but would not be recognized as a cap cell, as in some species of *Brickellia*.

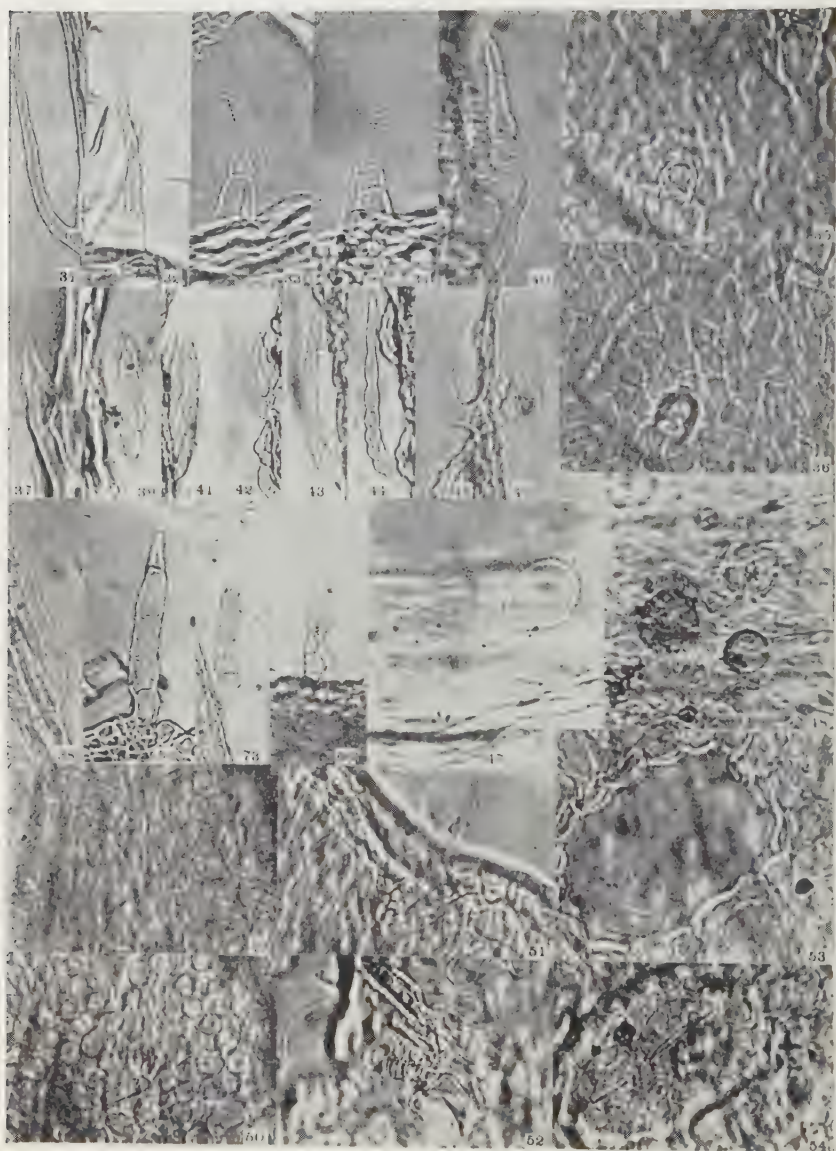
On no leaf preparation examined of any of the species of *Kuhnia* was evidence seen of the biseriate glandular trichome. By contrast the depressed gland and punctate condition was common to all species except *K. adenolepis*, and to both surfaces of the leaf, though generally it was less abundant on the upper.

What in *Brickellia* had been called uniseriate capitate glands, on stalks only a few cells in height, prevailed in all species. Generally they were small as in that genus, requiring a larger magnification for observation as well as photography as shown in Figure 47, $1100\times$, of *K. Mosieri*. An

exception to the general was found in *K. adenolepis*. This species had been distinguished by Robinson (1911b) because of its unique glandular ciliate phyllaries, the glands being described as sessile and black. The leaves had been described as "punctulatis" on both surfaces. Very short trichomes have been described for the upper surface (Fig. 37). Examination of a cleared preparation of the type specimen revealed more abundantly on the lower surface, a gland that is a little larger than the previous (Fig. 48, 530 \times) and distinctive for its dark apical cell when the leaves of all species had been cleared similarly. It is possible that the apical or secretory cell in this species has a different content, as not only was it dark but as shown in the figure some of its secretion had plugged and darkened some of the sunken stomata, from which it had not completely dissolved. From the very evident secretory function of the apical cell of this uniseriate small type of trichome, which is so similar in form to that seen in *Brickellia* (Fig. 87, 88, Gaiser 1953), I have considered them glandular trichomes in these two genera as did also G. Fischer (according to Solereder 1908, original thesis not seen). Vuillemin (1884) had done likewise in *Cynara* and *Echinopus*, though there are no figures of those for comparison. They are quite unlike the bladder-like trichomes observed by Volkens (1887) in *Zollikoferia nudicaulis*, which are considered to be full of cell sap (Solereder 1908, Fig. 103E). In form, they resemble somewhat more the capitate hairs described by Rosenthaler and Stadler (1908, Fig. 28) for *Cnicus benedictus*, consisting of six to twelve cells, with an elongated terminal cell which were said to differ from the non-glandular hairs in having a richer content.

Two genera, *Garberia* and *Carphochaete* had been established as having entire leaves. Neither the single species of the first nor any of the four of the latter had trichomes comparable to those illustrated for the previous genera. They both had a more slender filamentous form somewhat prostrate over the surface of the leaf.

When Bartram first described *Garberia* under the name *Cacalia heterophylla* (see p. 90), he wrote of the fleshy leaves: "of a pale whitish green, both surfaces being covered with a heavy pubescence and vescicular, that when pressed feel clammy and emit an agreeable scent." It was no surprise then when both surfaces gave the familiar appearance of the punctate condition at a focus when stomata were clearly visible (Fig. 49) and of the paired hemispherical cells of the depressed gland (Fig. 50) by sub-surface focusing. In addition, very narrow delicate filaments which tapered slightly if at all, and had cross walls at rather long intervals, lay twisted over the epidermis and proved difficult to follow to their origins. When the margin of this thick, entire leaf was examined it was possible by careful focusing to follow the epidermis as it alternately rose and fell into small pocket-like areas. In each depression was a tiered organ, two cells wide and approximately six cells high (Figs. 51, 52) familiar as the glandular trichome seen upon the leaf-surface of *Barroetia glutinosa* (cf. Fig. 33). In *Garberia* these arose in the epidermal layer from smaller cells which were clearly differentiated by their size. The first cells above

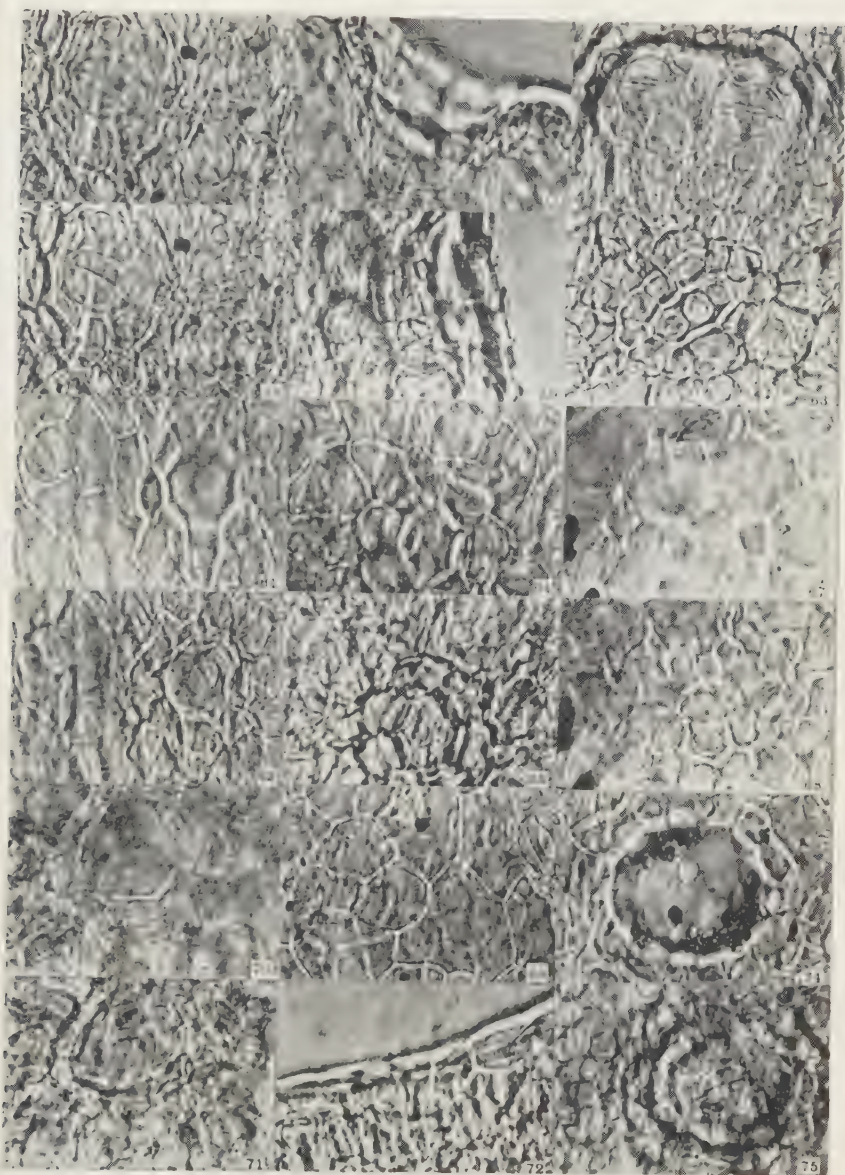


EXPLANATION OF FIGURES OF TRICHOMES

Figs. 31, 32, 37-46, 44-53, 56, 73. Non-glandular trichomes. Figs. 33-36, 66. Glandular biseriate trichomes. Figs. 47, 48. Non-glandular uniseriate trichomes.

31. *Barroetia sessilifolia*. 32. *B. subuligera* var. *latisquama*. 33-36. *B. glutinosa*. 33, 34. Along the leaf margin. 35. Above the epidermal surface. 36. At the epidermal surface. 37. *Kuhnia adenolepis*. 38. *K. Mosieri*. 39. *K. Schaffneri*. 40. *K. rosmarinifolia*. 41-44. *K. eupatorioides*. 41. of variety *pyramidalis*, 42. of var. *texana*, 43. of var. *ozarkana*, 44. of var. *corymbulosa*. 45. *K. leptophylla* var. *mexicana*. 46. *K. oreithales*. 47. *K. Mosieri*. 48. *K. adenolepis*. 56. *Carphephorus corymbosus*. 66. *Trilisa paniculata*. 73. *T. carnosa*.

All these photomicrographs were made from cleared leaves by use of a Zeiss microscope and a Homal IV lens, except Fig. 32, which is 110x. Figs. 38-46, 56, 66, 73, 85x. Figs. 31, 33-37, 48, 200x. Fig. 47, 430x.



EXPLANATION OF FIGURES OF DEPRESSED GLANDULAR TRICHOMES

Figs. 49, 53, 57, 61, 64, 67, 69, 70, 74, by focusing at the epidermal surface. Figs. 50, 54, 58, 60, 62, 63, 65, 68, 71, 75, by focusing below the epidermal surface. Figs. 51, 52, 55, 59, 72, lateral view seen along the margin of the epidermal surface of leaf.

49-52. *Garberia heterophylla*. 53-55. *Carphochaete Bigelovii*. 57-60. *Carphephorus tomentosus*. 63-65. *C. corymbosus*. 61, 62. *C. bellidifolius*. 67, 68. *Trilisa paniculata*. 69. *T. odoratissima*. 70-72. *T. carnosa*. 74, 75. *Liatris punctata*.

All these photomicrographs were made from cleared leaves by use of a Zeiss microscope and a Homal IV lens. x200.

these had thicker walls which generally reflected the light more than the thinner-walled upper cells. Alongside such a trichome frequently a slender filament could be traced until it pushed up to the leaf surface. In Figure 52 part of such a filament is recognizable after it emerged above the leaf, though it is seen less clearly along the right wall of the small depression. Closer microscopic observation of the surface of the leaf then made intelligible what had been baffling in several other genera as well. In addition to the paired hemispheric cells seen when focusing below the surface, an additional small round cell (shown at the bottom in figure 50) accounted for the delicate emerging filament seen on the surface. Thus they are really very delicate uniseriate trichomes of long, narrow, thin-walled cells growing from the sunken epidermal layer alongside the biseriate glandular trichomes.

Volken (1890) described scattered groups of trichomes consisting of five or six which were uniseriate with whip-like tips, surrounding one central unstalked, biseriate, bladder-like gland (Pl. 8, Fig. 1) on the upper surface of the leaf of a plant labeled "*Baccharis Richardifolia*." A second species of the *Astereae*, *Olearia Hookeri*, was said to be very similar while on the other Compositae that he examined, the uniseriate elements were increasingly fewer. In two genera representing the *Eupatorieae*, *Eupatorium* and *Symphyopappus*, these trichomes might occur occasionally but lacked the characteristic thread at the tip. From his figure 4a, showing two hemispherical cells of *Symphyopappus*, it appears that the biseriate gland was depressed with only the uniseriate emerging above the surface. Thus while the latter (Fig. 4b) appears more torulate, the grouping might be similar to that described here for *Garberia*.

Carphochaete Bigelovii had been described by Gray (see p. 90) as puberulous and resinous punctate. On first examination of the leaf preparation with lower magnification, very numerous depressed areas were seen which were not all equal in size. Closer examination of one of the smaller, revealed besides the two large appressed hemispherical cells, several accompanying small round ones as the one seen in *Garberia*. The delicate filaments, of which the latter are the bases, were not as long and therefore did not appear as abundant over the surface. The larger areas might merely show central cells of a greater diameter but frequently they were the result of the confluence of two pairs (Fig. 54). In this figure there are in addition, the bases of three filaments, two of which are seen at the surface in figure 53. Since the leaves of this species are small but rigid it was possible again by focusing along the margin of a prepared leaf to obtain a lateral view of the gland (Fig. 55). Only the lowermost pair of cells were thick-walled in comparison with the several in *Garberia*. The walls of the cells immediately above were very thin and made it difficult to show that there was but one intermediate pair. It was clear that the uppermost secretory cells were very much expanded, thus contributing to their larger surface-appearance.

Although one of the four known species, *C. Wislizeni*, had been described as "not sprinkled with resinous dots," a leaf of a Pringle specimen

(#765) from the mountains near Chihuahua, where the type was collected, was found to be very similar to *C. Bigelovii*. All four species might differ slightly in the abundance but not in the form and the kind of contents in the depressions.

The species of *Carphephorus* may have the small, upper cauline leaves pubescent when the lower and radicle leaves are nearly glabrous. This is not a character peculiar to the genus. Solereder (1908) having generalized that in many genera only the youngest leaves, branches and leaf petioles are covered with glandular trichomes. Thus much would depend upon the choice of leaf for preparation. Of *Carphephorus*, in common with the other genera, lower larger leaves were examined, leaving to *Trilisa paniculata* the comparison of lower and upper ones.

In form, the non-glandular trichomes on the surfaces and along the margin of the basal leaves of each of the four species of this genus were of near uniform type, of broader cells than seen in species of *Kuhnia*. Though they varied in length and to a minor degree in thickness of wall, being thickest in *C. tomentosus*, the cylindrical shape of the component cells was remarkably constant. One of medium length of *C. corymbosus* is illustrated (Fig. 56).

It was in the punctate condition of the leaf that a greater difference was noted, as is reflected in the descriptions given by Torrey and Gray (1841): *C. tomentosus*, punctate; *C. pseudo-liatris*, sparsely punctate; *C. bellidifolius*, punctate with scattered impressed dots; *C. corymbosus*, sometimes obscurely punctate. From these phrases it was not clear whether the difference was merely one of abundance. Examination of these leaf preparations showed a considerable difference in glandular structures.

On either surface of a lower cauline leaf of *C. tomentosus*, the paired cells characteristic of the depressed gland were seen abundantly when focusing below the surface (Fig. 58) in contrast to the craters seen when stomata are in view (Fig. 57). As described in *Garberia heterophylla*, the two hemispherical cells were accompanied by small marginal circular cells which had been recognized as the median optical view of delicate filaments. Frequently two or three were found and since they appear in figure 57 they obviously reach the surface though none were found spreading over the epidermal cells. Looking along the margin of one of these lower nearly glabrous leaves which is entire, the lateral view of the biseriate trichome with accompanying filaments at the side was seen in the depressed areas (Fig. 59). To this species then, the term punctate, as understood for the previous genera, could certainly be applied. The depressions were conspicuous macroscopically and that may be facilitated by their greater size for it was found that often two glandular trichomes, each with several laterally placed filaments were within the margin of one depression (Fig. 60).

In the preparation of the other three species the surface pattern appeared quite different. In a similar leaf of *C. bellidifolius* there was no sign of the depressed gland of paired cells. Instead, one circular cell,

TABLE III
Types of Trichomes and Glands in the Epidermis of Leaves of Genera of *Kuhniinae*

Name	Elevated above the surface					Depressed (i.e., punctate)								Depressed (but not punctate secretory, uniseriate upper lower
	Non-Glandular					Glandular								
	uniseriate, trichomes	uniseriate, capitate		Biseriate		Biseriate		Biseriate uniseriate		uniseriate in groups 1 to 4		uniseriate upper lower		
	upper	lower	upper	lower	upper	lower	upper	lower	upper	lower	upper		lower	
<i>Barroetia sessilifolia</i>	acuminate													
<i>B. subuligera</i> var. <i>latissquama</i>	acuminate													
<i>B. laxiflora</i>	acuminate													
<i>B. brevipes</i>	acuminate													
<i>B. setosa</i>	acuminate													
<i>B. glutinosa</i>	occasional													
<i>Kuhnia eupatorioides</i>														
var. <i>pyramidalis</i>	nearly uniform													
<i>K. eupatorioides</i>	attenuate towards													
var. <i>texana</i>	moniliform													
<i>K. eupatorioides</i>														
var. <i>oxarkana</i>	ditto													
<i>K. eupatorioides</i>														
var. <i>corymbulosa</i>	scabroid moniliform													
<i>K. rosmarinifolia</i>	scabroid moniliform													
<i>K. Mosieri</i>	nearly uniform													
<i>K. Schaffneri</i>	attenuate													
<i>K. oreithales</i>	slightly moniliform													
<i>K. leptophylla</i> var. <i>mexicana</i>	scabroid moniliform													
<i>K. adenolepis</i>	scabroid moniliform													
<i>Carphochaete Bigelovii</i>	very short													
<i>C. Wislizeni</i>														
<i>C. Grahamei</i>														
<i>C. Schaffneri</i>														
<i>Garberia heterophylla</i>														
<i>Carphephorus tomentosus</i>	nearly uniform													
<i>C. corymbosus</i>	nearly uniform													
<i>C. pseudo-liatriis</i>														
<i>C. bellidifolius</i>														
<i>Trilisa paniculata</i>														
<i>T. odoratissima</i>														
<i>T. carnosia</i>	nearly uniform													

Types of trichomes as seen by microscopic examination of cleared leaves from

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Types of trichomes as seen by microscopic examination of cleared leaves from apices to bases of leaves.

larger than those accompanying the gland in *C. tomentosus*, appeared encircled by other leaf cells (Fig. 62). By focusing exactly on the surface, when stomata are visible, there was again a crater-like appearance in its place (Fig. 61). This gave confirmation that we were seeing the punctate equivalent for this species which had been characterized as "compressed dots," likely because they are smaller.

In *C. corymbosus* a similar arrangement of cells was characteristic but the center was usually composed of more cells. Figure 63 shows a frequent linear arrangement of three. When there were four such cells they conformed to the arrangement common to four spheres and the surrounding leaf cells had a circular form (Fig. 65). At the epidermal level with stomata visible, this also had the appearance characteristic of a punctate condition (Fig. 64).

In several preparations of *C. pseudo-liatris* the little evidence seen of glandular punctation indicated similarity to *C. corymbosus*.

Thus all four species are punctate, indicating the presence of a depressed gland or short glandular trichome. In *C. bellidifolius* there was a single or uniseriate condition while in *C. corymbosus* and *C. pseudo-liatris* there might be from one to a group of four of the uniseriate form. In *C. tomentosus* there was the familiar biseriate trichome accompanied by the uniseriate similar to *Garberia*.

From the time of Walter's original descriptions of the two species of *Anonymos* (see p. 91), *Trilisa paniculata* has been distinct from *T. odoratissima* in having a viscidly pubescent stem and upper cauline leaves. For this reason some of the latter as well as the lower glabrous leaves and in addition phyllaries of the inflorescence of this species were cleared. On both the phyllaries and small leaves, typical biseriate glandular trichomes were found (Fig. 66) very comparable to that figured for *Barroetia glutinosa*. Examination of either surface of a basal nearly glabrous leaf showed neither these glandular trichomes nor any trace of the typical depressed gland of two hemispherical cells. Instead rosette-like arrangements around a central cell were seen when viewed at a sub-surface focal level (Fig. 68). This figure does not appear unlike that of *Carphephorus bellidifolius* (see Fig. 62). However, when viewed at the surface the epidermal cells clearly adjoin the specialized cell (Fig. 67). This is confirmed in figure 69 of *T. odoratissima*, photographed at the surface and showing more clearly the secretory droplets. There is no indication of any marked depression in the epidermis of either species. This explains the inclusion of "not punctate with impressed dots" in the description of section *Trilisa* Cass. of *Liatris* by Torrey and Gray (l.c., p. 76) since they included only these two species at that time. At the surface the specialized cell hardly appears to be free from the surrounding cells of the epidermis. However, the fact that a central cell remains in focus from that layer through the next below, which shows distinct encircling cells, indicates that it is a secretory organ with a greater depth than one epidermal cell. None of these distinctive cells was found close to the thin margins of the leaves of these two species and so could not be studied laterally as was possible

in the preparations of *Garberia*, *Carphochaete* and *Carphephorus tomentosus*.

Trilisa odoratissima, commonly named the Vanilla Plant for the fragrance of the crushed leaves, has been used in the tobacco industry and is included in lists of drug plants. Therefore references ⁶ to the study of the structure of its leaves have been found in pharmaceutical journals.

Paschkis (1879) was probably the first to study the leaves microscopically. He described the upper and lower epidermis as including yellow spots, .015 mm. in size, which were surrounded by regular small epidermal cells. From tranverse sections he found these to be glands, in small clefts, consisting of a basal stalk cell wedged in between the two adjacent epidermal cells, and three to four additional ones. These rise just to the level of the other epidermal cells. He makes a point of their close envelopment by the thick cuticle of .008 mm., and as his figures show, the small depression in the epidermis is closely filled. This undoubtedly explains my failure to see any crater-like opening over the gland in surface view. The secretion, which is of such a pleasant odor when expressed, is due to cumarin. The diagram in Higley (1893) is very similar to the above description as is also the figure in Hanausek (1912) who called it a glandular trichome. From the relation to the leaf surface it has its origin as a depressed form. Among the multiple types found in these genera it is here termed uniseriate and not punctate.

In the leaves of the recently added third species, *T. carnosa*, the frequent appearance of a single central cell was again replaced by the two characteristic of the depressed biseriate gland (Fig. 71). By focusing on the surface when stomata are in view, the crater-like appearance of the punctate condition was again shown (Fig. 70). By carefully following around the margin of the leaf for any traces of the gland, only near the apex where it was thicker, a lateral view of one was seen (Fig. 72) giving evidence of at least an occasional uniseriate gland such as found in the previous genera. Certainly when examined microscopically the large basal leaf of *Trilisa carnosa* appears very different from those of its two congeners. However, in a similar way the biseriate glandular condition of one *Carphephorus* species, *C. tomentosus*, distinguished it from the other three.

No non-glandular trichomes were found on the lower leaves of the first two species and only an occasional short one near the petiole of *T. carnosa*. They were very similar to those of *Carphephorus* (Fig. 73).

SUMMARY (RE TRICHOMES)

With the help of table III, the observations on trichomes and glands on basal cauline leaves can be summarized.

1. Non-glandular, uniseriate trichomes are lacking in *Garberia* and *Carphochaete* and show very little variation within three genera, being

⁶I am indebted to Prof. G. N. Hocking for these references.

acuminate in *Barroetia* and nearly uniform in *Carphephorus* and *Trilisa*. In *Kuhnia*, the largest of these genera, they may vary from being nearly filamentous or uniform to slightly tapering or attenuate. The thicker walled forms of the latter suggested the moniliform.

2. The elevated biseriate glandular trichome, comparable to that forming the indumentum in a number of species of *Brickellia*, was found only in one species of *Barroetia*.

3. The same structure sunken below the leaf surface, the depressed biseriate glandular trichome, was common to all the other species of *Barroetia* and to all species of *Kuhnia* and one of *Trilisa*.

4. In *Garberia* and one species of *Carphephorus* the same biseriate gland was accompanied in the depression by uniseriate but non-capitate glandular trichomes while in all four species of *Carphochaete* the same grouping occurred but the biseriate gland was different in form.

5. In the other species of *Carphephorus* uniseriate glandular trichomes were depressed either singly, in one species, or grouped, in two others.

6. The two other species of *Trilisa* were characterized by compact, depressed, uniseriate, secretory glands.

7. The small uniseriate capitate glands were observed only on species of *Kuhnia*.

8. As the punctate condition results from a depressed gland or glandular trichome it was found in all genera and all species except *Trilisa odoratissima* and *T. paniculata*.

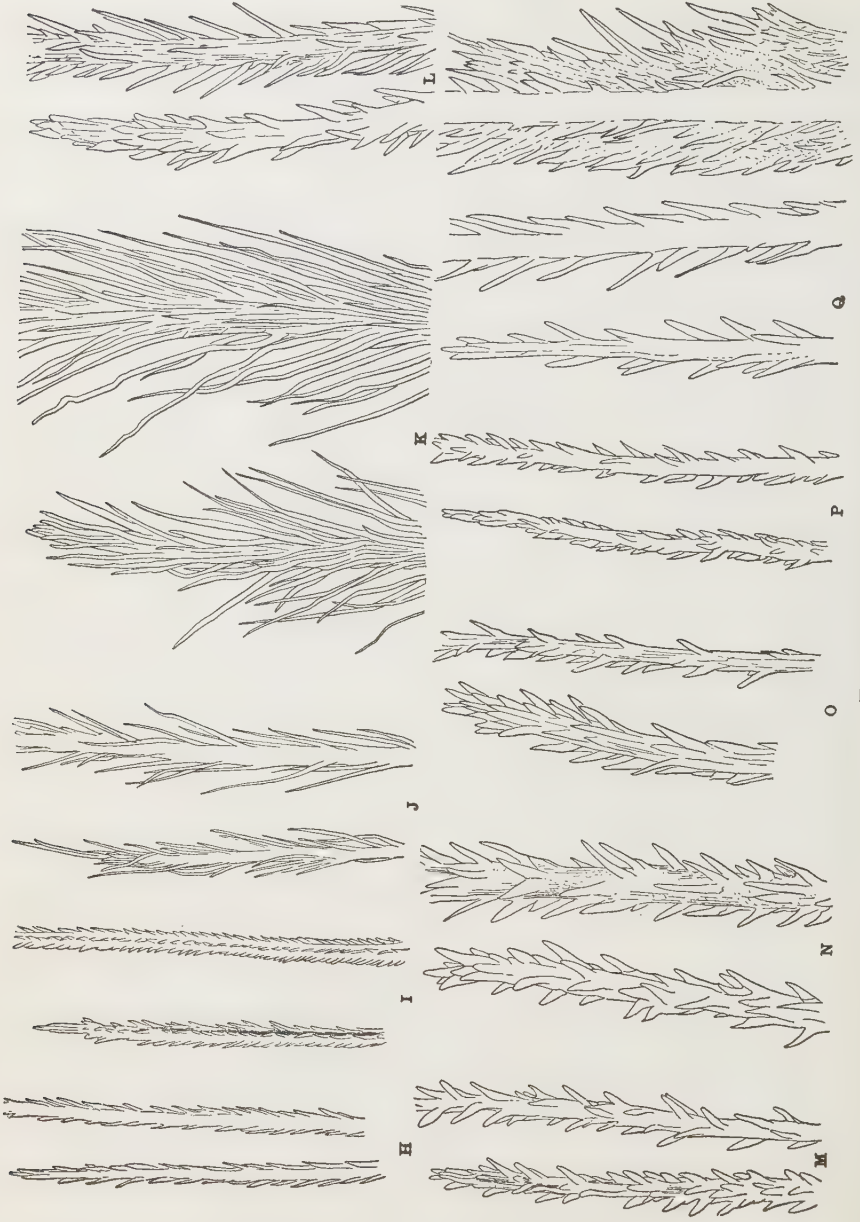
9. While in representatives of each genus, the depression contained the biseriate glandular trichomes, in three species of *Carphephorus* there were uniseriate trichomes singly or in groups. Thus the punctate condition accompanies different glandular contents in these genera.

A very reticulate pattern is evident in the distribution of the glandular trichomes. Though some form is found in every species, the same is not necessarily common to all those of any genus.

IV. Pappus

In the key to his treatment of this group of genera, Hoffmann (1890) made use of differences in the length of barbules of the pappus, besides the singular scale-like nature of that of *Carphochaete*. Thus *Kuhnia* was distinguished by plumose pappus from *Brickellia* and *Barroetia*. Illustrations of *Kuhnia eupatorioides* and *Brickellia californica* A. Gray (Fig. 81 B & C) were drawn to scale and indicate that for these two species, the barbules of the former are at least four times as long as the latter.

Robinson made little use of the pappus in the classification of *Brickellia* because he found that as well as in barbule-length, the number of setae varied widely from species to species. As pointed out (Gaiser 1953), Robinson did include its plumose nature under the sectional heading of *Steviastrum* and elsewhere only in the species-descriptions of *B. brachyphylla* and *B. monocephala*. Lactic acid mounts have confirmed a wide variation in the length of barbules of more than six times from these two



FIGURES OF PAPPI

which are the longest, to the shortest. Generally in any species the barbules become a little longer away from the tip of the seta. However, their arrangement in this genus seemed distinctive from that seen in *Liatris*. The generally flattened appearance along the greater length of the seta in many species resolved itself as a distichous arrangement of the barbules along the axis, as shown for *B. Nelsonii* Robinson (Fig. H). In other species, e.g., *B. Coulteri* where the barbules were only about half as long, their arrangement along the mid-portion of the seta approached the marginal appearance of the serrulate-paleaceous type of Small (1919, fig. 17H). However, the central axis in all the specimens seen did not broaden greatly, showing an increase in diameter of not more than twice with an elongation of barbules of three times or more than that amount. *Brickellia diffusa* and *B. filipes*, the two annuals, appeared exceptional in having the barbules arranged in three rows or tristichously. Always at the apices, the barely emerging barbules came in less regular arrangement and for this reason the illustrations include an apical as well as a median portion of a seta. In some species having short barbules, the irregularity persisted further along the axis.

Comparison of similar mounts of species of all of these genera here studied was therefore included. In contrast to the very large genus *Brickellia*, the smaller genera showed a greater uniformity in the nature of the pappus.

In *Barroetia* the length of the barbules varied little in the six species examined, being about equal to the shortest in *Brickellia*. Their arrangement also was uniform so that the seta had the appearance of a four-angled structure, due apparently to a tetrastichous arrangement of the barbules. In figure I, the row of barbules in the center below were not included. No exact equivalent for this was found in Small's figure 17 of pappus forms in the *Compositae*.

The plumose pappus of species of *Kuhnia* varied distinctly from *Barroetia* not only in the length of the barbules but also in the longer spaces between the points of their emergence from the axis and in their flat, distichous arrangement (Fig. J). In the latter they resembled *Brickellia*. In comparison with the plumose pappus of a species of *Liatris* (Fig. K) the barbules are slightly more slender and appear much less abundant because they do not extend from the mid-axis. Although the tips of emerging cells can be seen over the center region, they do not project laterally.

EXPLANATION OF FIGURES OF PAPPUS

All figures are of pappus from specimens in the Gray Herbarium and will be referred to by the collector's number, except Figs. M and N, *Trilisa paniculata* and *T. carnosa* which were of accessions studied cytologically, from Sebring, Highlands Co., Fla., Ray Garrett, Nov., 1948.

Fig. H. *Brickellia Nelsonii*, Nelson 4449. Fig. I. *Barroetia brevipes*, Nelson 1520. Fig. J. *Kuhnia adenolepis*, Pringle 2933. Fig. K. *Liatris squarrosa* var. *glabrata*, Rydberg 1505. Fig. L. *Liatris ligulistylis*, Nelson 1651. Fig. O. *Carphephorus tomentosus* var. *Walteri*, Fernald and Long 11173. Fig. P. *Garberia heterophylla*, Nuttall. Fig. Q. *Carphochaete Schaffneri*, Schaffner, 241.

The author is greatly indebted to Dr. B. G. L. Swamy for these figures, drawn $\times 45$.

This is indicated in another illustration of *Kuhnia eupatorioides* (Hoffmann 1889, Fig. 60D) where it can also be compared with *Liatris pycnostachya* Michx. (Fig. 60B), which has a barbellate pappus. At least five of the seven species of *Kuhnia* had barbules of approximately the same length, while those of *K. leptophylla* var. *maxima* and *K. adenolepis* were from half to three quarters as long. In length the barbules of this majority are somewhat intermediate between that of *Liatris squarrosa* (L.) Michx. var. *glabrata* (Rydb.) Gaiser, belonging to section *Euliatris* with plumose pappus and *L. ligulistylis* (Nels.) K. Sch., of section *Suprago* in which it is barbellate.

While it is difficult, when the barbules are as long and as abundant as in the plumose pappus of *L. squarrosa* (Fig. K) to illustrate their points of emergence even at the apex, when they are shorter as in the barbellate type of *L. ligulistylis* (Fig. L), their general disposition all around the axis is evident. This is similarly shown in the figure of *L. pycnostachya* of Hoffmann (l.c.). The projecting barbules are not limited to two sides and give no suggestion of a flattened appearance. They emerge somewhat spirally as shown also for this type (Small fig. 17D). This same arrangement was seen in the mounts of species of *Trilisa* (Figs. M & N), *Carphephorus* (Fig. O) and *Garberia* (Fig. P) all of which have barbellate pappi with barbules shorter than those of *Liatris ligulistylis* though equal to those of some other species, e.g., *L. gracilis* Pursh. Except for slight variations in the length of the barbules, the similarity of the pappus from genus to genus, as well as of the species within a genus was too great to allow any differences of classificatory value for *Trilisa*, *Carphephorus* and *Garberia*.

Of course, *Carphochaete* with its paleaceous pappus is quite distinctive from all the others (Fig. Q). It is dilated and scale-like at the bottom and for this reason the figure of this form includes a basal portion in addition to the median and apical. *Carphochaete Schaffneri*, the species illustrated, has the shortest free barbules at the apex of any of the four. The two other Mexican species are very similar to it, while in *C. Bigelovii* they are almost twice as long.

DISCUSSION

This study of six genera indicates a relationship with the two others previously studied, *Brickellia* and *Liatris*. With the exception of *Kanimia*, of which it has been impossible to include cytological examination and therefore discussion has been omitted, there is support for the taxonomic grouping of the subtribe *Kuhninae*. *Kanimia* will have to be compared cytologically with *Mikania*, the genus of the previous subtribe *Ageratinae*, with which it may well be a connecting link because of the several technical characters which the two genera have in common.

Furthermore, some points of relationship within the subtribe have been

added to those noted by earlier authors. These have served as a guide in the preparation of a key (see p. 124) which attempts to more nearly approach a natural classification. It has already been pointed out that when Cassini established each of the two new genera, *Carphophorus* and *Trilisa*, he placed them next to *Liatris*. Also because of the strong similarity of the flowers, Nuttall first described *Garberia* as a shrubby *Liatris*. With the additional evidence gained from the study of seedlings, trichomes, pappi, and chromosome numbers, it is proposed to refer to these four genera as Group I.

Likewise there is sufficient evidence to warrant a second grouping. When Gray (1879) established the genus *Barroetia*, he began the description "Involucrum (15-25) flores *Kuhniae* et *Brickelliae*." Hoffmann (1890) in his introduction to the subtribe also referred to *Barroetia* as approaching *Brickellia* in all else except the nature of the fruit. Robinson, who monographed both these genera, re-emphasized their strong similarity in habit and involucre, giving the flattened achene and sharply toothed leaves as the chief points of difference. To separate *Kuhnia* from *Brickellia*, the same author referred to its less strongly imbricated phyllaries and plumose pappus. For Shinnars (l.c.) these technical characters were not completely satisfactory, as was also an additional one, the nature of the root system. His conclusion was that though separately imperfect they were "strengthened by the obviously close relationship of the species of *Kuhnia* to each other, making a closeknit and recognizably distinct group." The association of these three genera will be continued as Group II.

Even in the seedling stage, at least as they grew in the greenhouse, differences were noted which distinguish the two groups. Those of species representing Group I, had a rosette of leaves which persisted without production of a flowering stem for a longer period than would necessarily be required for a biennial. In seedlings of *Garberia*, the one shrub of the group, this stage did not last as long and then a central leafy stem began to appear though it never flowered. However, species of Group II, including representatives of all three growth-forms, e.g., annual herb, perennial herb, and shrub, produced elongating central axes almost at once and these flowered before the end of a year. The seedlings of *Carphochacte Bigelovii* resembled the members of this latter group.

It was felt by Shinnars that in distinguishing *Kuhnia* undue reliance had been placed on the plumose pappus because it might not be the exclusive type of a genus, e.g., *Liatris*. From an examination of the pappus of these genera by lactic acid mounts, it was found that the arrangement of the barbules differed in these two. Further, though the barbules were longer in *Kuhnia* than in species of *Brickellia*, their lateral arrangement was more nearly like the distichous pattern found in the majority of the species of that genus. In two species of *Brickellia*, the three-sided or tristichous arrangement suggested a mid-way condition between that of the others and that typical of *Barroetia* where it was four-sided or tetra-

A GENERIC KEY TO THE KUHNIAEAE⁷

Anther apex having an ovate or oblong membranaceous appendage, achenes 10–20 (rarely 6–9) ribbed, phyllaries indefinite in number.

(a) Pappus squamiform, dilated at the base, small shrubs, leaves opposite, young plants without rosettes, corolla rose-colored or white, chromosome number $n = 11$ **Carpochaete**.

(a) Pappus setose.

(b) Phyllaries not conspicuously striate, leaves alternate, young plants with rosettes, corolla rose-colored, rarely white, barbules of pappus indefinitely arranged along the axis, chromosome number $n = 10$ **GROUP I**

(c) Woody shrubs, leaves alternate obovate, rosette-form not persisting long, phyllaries herbaceous, pappus barbellate **Garberia**.

(c) Perennial herbs, leaves linear to lanceolate, rosette-form persisting. (d) Receptacle chaffy, phyllaries subequal pappus barbellate

..... **Carphephorus**.

(d) Receptacle naked.

(e) Plants arising from thickened fibrous root-system, phyllaries 2–3 seriate pappus barbellate **Trilisa**.

(e) Plants arising from a corm-like or deeply penetrating root-system, phyllaries imbricate, herbaceous or colored or scarious, pappus barbellate or plumose **Liatris**.

(b) Phyllaries thin, striate, scarcely herbaceous, leaves alternate or opposite, young plants without rosettes, corolla ochroleucous to yellow, rarely rose-colored, barbules of pappus tend to be in linear arrangement along the axis, chromosome number $n = 9$ **GROUP II**

(f) Achenes prismatic or rounded.

(g) Phyllaries imbricate in several series, shrubs and perennial, rarely annual, herbs, pappus tends to be arranged distichously, rarely tristichously ..

..... **Brickellia**.

(g) Phyllaries 2–3 seriate, perennial herbs from long conical roots, pappus plumose, barbules arranged distichously **Kuhnia**.

(f) Achenes compressed, annual and perennial herbs, barbules of pappus arranged tetrastichously

..... **Barroetia**.

stichous. Thus in the pappus of the two smaller genera, in comparison with *Brickellia*, the arrangement of barbules alone differentiates *Barroetia*, and arrangement in addition to length, *Kuhnia*. While interspecifically *Brickellia* shows considerable variation in length of barbules, the species have the same basic linear arrangement which adds support to the placement of these three genera in one group. Similarly the four genera of Group I resemble one another in a less definite, somewhat spiral arrangement of the short barbules as is shown in figures of setose pappus.

In addition to the characters in prevalent use by taxonomists, it has been noticeable that in the *Eupatorieae*, it was necessary to pay consider-

⁷ Exclusive of *Kanimia*.

able attention to glandular structures. Robinson had established species as well as varieties on the presence of glands on the phyllaries, e.g., *Kuhnia adenolepis*, *Brickellia adenocarpa* var. *glandulipes*, etc. Likewise Brandegee (1908), who described two of the seven species of *Barroetia*, found *B. glutinosa* "differing from the others of the genus" because of the glandular leaves. Also, the common use in manuals, as well as descriptive treatises, of the term punctate and punctulate in some species, left open the question of general application for all of each genus. As explained under *Brickellia*, there was the need for interpretation of the overlapping use of the various terms applied to the depressed glands and the punctate condition. A more detailed comparison than had been possible by macroscopic examination, has helped to clarify.

From the reticulate pattern of glandular trichome distribution in six genera, summarized in Table III, and of *Brickellia* (Table III, Gaiser 1953), it was seen that some form was represented in each species. *Liatris* also can come in this inclusive statement. In the introduction to the treatment of that genus, it was stated that small sunken resinous glands were generally found in the leaves of species. Examination of cleared leaves of at least several species have given confirmation of the presence of the depressed biseriate trichome in connection with the punctate condition, as shown for *L. punctata* (Figs. 74, 75). A closer analysis of these tables gives indication of some intergeneric similarities.

In several species of *Brickellia*, the pubescence consisted almost entirely of the biseriate glandular trichome. That, of all the species of the other five genera examined, only puberulence of one species of *Barroetia* was composed of this form, is another point to add to the number in which that genus strongly resembles *Brickellia*. However, in the thick leaf of *Brickellia glutinosa*, a similar shorter biseriate trichome was shown to make up the depressed gland which gives a surface appearance of only two hemispherical cells as seen in species of *Kuhnia*, as well as the other species of *Barroetia* and *Brickellia*. The conclusion was reached from the range of variation seen in the extent to which the biseriate gland rose above the surface in different species of *Brickellia*, that the superficial glandular trichome was an elevated expression of the depressed gland. With the additional evidence in the fleshy leaves of the other genera of the heights it may attain and still remain macroscopically subsurface, there is no reason to doubt the generality of the statement. It is as understandable that the height of this small organ should vary in leaves of different species as that non-glandular trichomes should vary in length. More important than the variation from a depressed to an elevated condition may be the uniformity of this biseriate glandular organ. While these three genera of Group II have in common this single, similar content in the depressions in the epidermis of the leaf, the four genera of Group I have mixed contents of biseriate and uniseriate, grouped or single uniseriate, or single uniseriate without correlation to the punctate condition.

Examining this apparent diversity, there is a link with the previous three genera in *Garberia* and one species of *Carphephorus* having this

same biseriate form in the grouping along with the uniseriate. To these, the other *Carphephorus* are tied in having only uniseriate trichomes and *Carphochaete*, in having uniseriate with a different form of biseriate trichomes. Likewise in the two species of *Trilisa* the uniseriate trichome, though not accompanied by leaf punctation, appears similar in form to the depressed of *Carphephorus bellidifolius*, while *Trilisa carnosa* has the depressed biseriate resembling those of Group II. Thus while there is greater uniformity in the three genera of Group II, those of the other group seem to have a similitude in intra-generic variations. The particular form of the biseriate depressed gland of *Carphochaete* is individual among them. While its difference sets it apart from the genera of both groups, the true significance of this variation may be better understood when further knowledge is obtained of the forms in the many genera of other subtribes.

Further emphasis on relationships by glandular structures in these genera was found in the fact that there was a smaller, uniseriate, capitate trichome, which would not be readily observed without a microscope, along the veins and under surface of leaves of species of *Brickellia*. The only other genus of the subtribe studied to which it has been found common is *Kuhnia*. A slightly enlarged form apparently became the specialized type of *K. adenolepis*.

From a consideration of the non-glandular trichomes⁸ the largest genus has the widest variety. Comparable preparations of other genera contributed no distinctly new type, though in *Carphephorus*, *Trilisa*, and one species of *Kuhnia*, they were more nearly uniform in diameter and tapered a little less than the attenuate form shown for *Brickellia*. That all the types seen in that genus were not represented in the smaller genera could be explained probably by the smaller total of species. However, in *Brickellia* considerable variation was found in the size of chromosomes and in some subsections a correlation with the types of trichomes.

Cytological evidence has been obtained of some species of each of the genera of the *Kuhniinae* except *Kanimia*. Though incomplete, it supports the conclusions obtained from other sources. The basic number of chromosomes is 10 in the four genera of Group I, 9 in the three genera of Group II and 11 in *Carphochaete*. While no other genus of the subtribe has the same number as *Carphochaete*, the fact that the three basic numbers vary only by one, may be taken as further indication of a fairly close relationship of the members of this subtribe. This seems more significant when the number of species examined for the several genera to which the same number is common, totals forty-seven with $n = 9$, and thirty-nine with $n = 10$. Of course these two chromosome numbers are represented many times in genera of the Compositae as can be seen in Darlington and Ammal (1945, p. 220) where the basic numbers of the tribes of the Compositae are given. When turning to the reports for the tribe *Eupatorieae*, of which there have been few so far, the number 11 does not appear. The recent addition by

⁸ Gaiser (1946) in referring to pubescence as being of little use for species differentiation in *Liatis*, had not made microscopic analyses and there has not been time as yet to do so for that genus.

Grant (1953) of numbers for at least thirty-two species of *Eupatorium* from the temperate zone, give 10 and 17 as the lowest numbers, and 9 for one tropical species of *Vernonia*. The number 11 does not appear. This does present a challenge to investigate *Kaninia*. Also it raises the question of possibly finding the same number in a genus of another subtribe which perhaps may show further intertribal relationships with *Carphochaete*.

Of two species of *Mikania*, the genus of the previous subtribe *Ageratinae*, which has characters in common with *Kaninia*, it was possible to obtain some seeds (see Table I). The somatic chromosome number of three accessions of *Mikania scandens* Willd. and one of *M. cordifolia* (L.) Willd. was found to be $2n = 38$ (Fig. 21), which is quite different from that in any of the *Kuhniiinae* investigated. Thus it seems quite probable that cytology might give the deciding evidence for or against the segregation of these two genera within the same subtribe.

No lower basic number was found among these genera than had been found in *Brickellia* and *Liatris*, or had been known previously among the *Eupatorieae*. These numbers, 9 and 10, are higher than have been found in a number of the other tribes of the Compositae, e.g., *Chichorieae* with 3, *Heliantheae* and *Astereae*, with 4, *Inuleae* and *Senecioneae* with 5, etc., but this may find its explanation in the few genera studied. Of the *Kuhniiinae*, the genera of Group II with Mexico as their geographic center of distribution, have the lower number 9, while those of Group I, which are to the north of the Mexican boundary have 10. At this time there is no evidence of the origin of these divergent genetic lines. So far, the most northerly genus, *Liatris*, and in that only the *Punctatae* series, remains the only one in which polyploidy has been found. The tetraploid, *L. punctata*, reaches the most northerly latitude of any species of that or any other genus of the subtribe and so exemplifies Hägerup's theory. Since the same species reaches the southern extremity of the range for the genus along the mountains and the diploid is found on the plains in between it also provides an example of the polyploid occupying a wider area than the diploid. Müntzing (1936) believes that the extensive range is the combined result of polyploidy and polymorphism which has enabled adaptation to a wider range of habitats some of which may be unfavorable. Of all the other genera of the *Kuhniiinae* few include any species of very extensive range and none which is exactly comparable to *L. punctata*. *Kuhnia eupatroioides* is the only polymorphic species of that genus, occurring in the central states from the northern to the southern boundaries, Michigan to Texas, and from Kentucky to Montana in the west. In his introduction, Robinson referred to *Brickellia grandiflora* and *B. californica* as the two most widely distributed and variable species. Both were found to be diploid in these studies which included a generous representation of thirteen accessions of the latter species. The former species like two others studied, *B. microphylla* and *B. oblongifolia* reach the northern limit for that genus in Washington State, but they also were diploid.

Excepting the species of *Brickellia* in Brazil, the most southerly one from Costa Rica, *B. argyrolepis*, was also a diploid. For the discussion

of the polyploid complex and tropical plants, as pointed out in the introduction, this genus is somewhat exceptional since though within the tropical latitudes the species live on higher altitudes. Of *Barroetia*, which at similar altitudes does not extend north of Mexico, neither of two species were polyploid. Also one species of *Kuhnia* from the southerly limits for that genus was diploid like the three congeners from the United States. The conclusion from this discussion still remains that for these closely related genera, as they have been represented from Central America northward, polyploidy was not prevalent and occurred only in the most northern genus of Group I. However, variation in the size of the chromosomes was noticeable and the karyotypes of the shorter units occurred only in the genera of the more southern group.

This does not mean that we should not expect polyploidy in genera of the tropics. For comparison, in the tropical genus *Anthurium*, of which thirty-seven of four hundred and eighty-six species (Engler 1905) were examined from plants as they grew mostly in the New York Botanical Garden, the situation is quite different. While many additional species have also been added since Engler's monograph of the genus, there is indication that polyploidy is not singular and occurs in species of both limited and wide distribution (Gaiser 1927). With 30 as the lowest somatic number found, at least two other numbers of a polyploid series were represented, two species with ca. 50 and three with ca. 60. The five polyploids were distributed to as many different sections, some nearly monotypic and others, the largest of the genus, e.g., *Urospadix* with ninety-five species. *Anthurium radicans* which belongs to the section, *Chamae-repium*, comprising two species, is limited to east Brazil, and *A. Wallisii* of section *Polyneurium* of thirty species had been reported as having been collected only once in Colombia. In comparison with tetraploid *A. crassinervium*, from Venezuela, Colombia, Panama, and Tobago Island, nine other diploid species of the second largest section *Pachyneurium* with fifty species were found to be fairly restricted. Two species of section *Urospadix*, very similar to the polyploid *A. digitatum* from Venezuela and Tobago Island, had been collected from comparable areas. However, the fifth, *A. scandens*, is the most variable species in the genus, including five varieties and is known in one of its forms wherever Anthuriums grow. With even but fractional representation studied cytologically, all the complexities of polyploidy in percentage of incidence, different multiples of numbers and correlation of geographic distribution occur in that genus. Also, since Grant (l.c.) found fifteen polyploids (almost fifty percent) among the northern Eupatoriums examined, others might be expected among the many more tropical species of that large genus.

While the studies of *Liatris* were of a different time and were not all accompanied by exactly comparable photographic figures, chromosomes of the series *Spicatae* (Gaiser 1949) were considered to be the longest and to show greater variation than those of the series *Graminifoliae* (ibid. 1950a) and *Punctatae* (ibid. 1950b). Reference to the analysis of the morphology of the chromosomes of *L. pycnostachya* (1949 p. 127) gave

two pairs of long chromosomes in the karyotypes of 2 Lm, 2 Lst, 4 Mm, 4 Msm, 2 Mst, 4 Sm, 2 Sst. In the more recent comparisons the few species of the smaller genera of Group I varied little if at all from species to species. Also, the generally similar karyotypes of *Trilisa* and *Carphephorus*, including three pairs of long chromosomes, were found to vary somewhat from *Garberia* only in the types of the short and medium chromosomes. By comparison, *Carphochaete Bigelovii* was the only species to have a greater number of long chromosomes, four pairs rather than three.

Brickellia with the greatest number of species, had a great variation in chromosome sizes. Of thirty-four species in which the karyotypes were carefully analyzed, nine had only short and medium chromosomes, while in all the others there were also long ones. From the analyses of species of all these genera, only those of *Kuhnia* and *Barroetia* had such a karyotype of the two classes of shorter units. Thus not only have these three genera the same number in common but like a minority of the species of *Brickellia*, the species studied of the two smaller genera, have chromosomes representing an amount of chromatin less than is found in any of the others.

While too few species of *Barroetia* have been examined to draw conclusions regarding that genus, more than half of those of *Kuhnia*, including all but one variety of the polymorphic species *K. eupatorioides* have been included. The great homogeneity in the karyotype as well as chromosome number for all of these, shows a genetic basis for the close relationship of species of *Kuhnia* to each other, pointed out by Shinnars. By contrast the great diversity in chromosome length found in species of *Brickellia* accompanies a diversity of growth from woody shrubs to herbaceous annuals. None of the genera of Group I can compare with this. In *Liatris*, the largest of them, all the species are herbaceous perennials of a fairly similar type.

In the discussion of *Brickellia*, it was pointed out that a minority of the species examined, nine out of thirty-four, had a complement of shorter chromosomes. The species at the opposite extreme having the longest chromosomes, *B. monocephala* and *B. grandiflora*, were considered by reason of their modified underground structure, etc., as belonging to a specialized group of that genus. Others next to them, also having a greater total of chromatin material by reason of longer chromosomes than in the major group, included shrubs and herbs native to Costa Rica, Guatemala and Mexico. With the most woody species from Costa Rica among these, and the one annual examined, in the first group, there was some ground for considering that evolution had gone on in conjunction with reduction in chromatin in that genus. It is of interest therefore that the only other genus including annuals, *Barroetia*, also had short chromosomes in the two species examined. The genus includes no true shrubs and only one perennial variety of a species that has been described as being somewhat woody at the base. *Kuhnia*, too, is a genus consisting entirely of perennials and in it there was found a similar karyotype of the two shorter classes of chromosomes. While it is impossible to trace the steps of evolution from

one genus to another with certainty, it is indicated from the present evidence that the direction at least, was from *Brickellia* to the two other genera through some form, not necessarily extant today, having a complement of shorter chromosomes. Whether this happened in two successive steps or at one time remains a question also. The fact that both genera still include few and, for the most part, less variable species indicates that they are more recent than *Brickellia*. The repeated reference to the close similarity of *Barroetia* and *Brickellia*, especially as seen in both including annual species, suggests that there are possibly blocks of genes common to these two and this could have been one mutation. Also the indecision regarding basic differences between *Kuhnia* and *Brickellia* gives weight to the probability that this might have come as another step. The similarities of each of the two smaller genera to *Brickellia* appear closer than the interdependence of all three. Yet, as has been pointed out, from karyological studies, the six species of *Kuhnia* and two of *Barroetia* had karyotypes consistently represented by a pair of satellite chromosomes. Only in three, of about half of the species of *Brickellia* examined, was this type of chromosome regularly visible. Two of these were xerophytes. *B. incana* and *B. Greenei*, very restricted in distribution and remarkable for their large heads and seeds which are distinctive. The third was *B. Coulteri*, from Baja California, the only species examined of subsection *Brachiatae*. Most of the other seven species have been reported but once and from widely separated regions in Mexico and certainly should be compared cytologically. Without complete representation of a genus, the species not studied may be the ones which withhold the most significant truths. Perhaps the best that can be expected is to gain at least a point of vantage from which to envision the horizons for further efforts in a project.

It is difficult to extrapolate true phylogenetic relationships within Group I. In all four genera the karyotype is made up of more closely approximating units than were seen within the one genus *Brickellia*. Some variation has been reported in the species of five series of the genus *Liatris*⁹ but is not as striking as has been found in *Brickellia*. There was no evidence of marked morphological changes or reduction in size of the chromosomes. Also there is a general similarity of karyotype in the two smaller genera *Trilisa* and *Carphephorus*, including three pairs of long chromosomes. From these, *Garberia* was found to vary only in the medium and short chromosomes. Likewise, except for this one shrub *Garberia*, there is a greater homogeneity in the growth-form represented by each of the three genera. They are herbaceous perennials, provided with excellent modified storage rootstocks, mostly corm-like in *Liatris* and more tuberos in *Trilisa* and *Carphephorus*. From the discussion pertaining to growth-forms in *Brickellia*, just such as these were considered to represent a form of specialization and, these may very well be from a more primitive type now extinct. In the one living species of *Garberia* may lie

⁹ A chromosome list will shortly be forthcoming for species of the other series except the *Squarrosae*, which Dr. Pauline Snure will contribute.

the hint of another more woody progenitor for the other three genera.

The dissimilarity of the karyotype of *Carphochaete Bigelovii* to the species of Group I lay in the fact that it was the only species to have two additional chromosomes, four long chromosomes instead of three and three short ones rather than two. These factors contributed to its having the greatest content of chromatin in any of the genera studied. Comparison of it with the unusually long chromosomes of *Brickellia monocephala* (see Fig. 30, Gaiser 1953) is favorable except for the extra pair of chromosomes. The singularity of its karyotype, supported by the distinct form of the biseriate depressed gland and the individuality of its pappus, is sufficient to set it apart from the genera of both Groups I and II. Yet the prime reason for its inclusion in the subtribe *Kuhniiinae*, the similarity of its anther and achenes, also gains weight in a proximal chromosome number and karyotype to that of Group I and in the actual presence of a depressed biseriate gland.

Without examining other genera having paleaceous pappi for comparison with *Carphochaete*, it would be premature to generalize on the evolution of pappus forms. That this small group of related genera may contribute to the overall study is indicated by the variety shown in the barbule-arrangement especially in the three genera of Group II. In *Barroetia* and *Kuhnia* there is near uniformity for the species of each genus, while in the more numerous species of *Brickellia* there is a variety of almost imperceptible changes. The general tendency is for a flattened, lateral arrangement of barbules in two rows. While the significance of their quadrate, linear arrangement in *Barroetia* is not clear, it may be but one of nature's experiments and so also the tristichous disposition in *Brickellia diffusa* and *B. filipes* may be a further shuffling of genes. However, since the latter species are annuals and since *Barroetia* is the only other genus including annual species, it would be in agreement with phylogenetic evidence to assume that the change in *Brickellia* was in the direction away from the flat or distichous arrangement. And if so, the latter referred to as bearing a marginal resemblance to the serrulate-paleaceous, could have been derived from the paleaceous or more foliar by reduction. This would be in agreement with the conception of Babcock and Stebbins (1937) for genera of the *Cichorieae* rather than the alternative hypothesis of Small (1916), that the paleaceous types result from the fusion of the simple scabroid setose which constitute the primitive type.

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MISCELLANEOUS MALAYSIAN NOTES

E. D. MERRILL

With one plate

MORACEAE

Ficus porteana Regel, Gartenfl. 11: 280. *t.* 372. 1862; Gagnep. in Le-comte, Fl. Gén. Indo-Chine 5: 774. 1928.

Ficus malunuensis Warb. in Perk. Fragm. Fl. Philipp. 196. 1905; Elm. Leaf.

Philipp. Bot. 1: 192. 1906; Merr. Enum. Philipp. Fl. Pl. 2: 56. 1923.

Ficus cordatifolia Elm. Leaf. Philipp. Bot. 4: 1250. 1911.

My attention was called to *Ficus porteana* Regel by Gagnepain's reference of certain Indo-Chinese material to it and by his reduction of *Ficus malunuensis* Warb. to it as a synonym. Regel's species, entirely overlooked by me when engaged in the preparation of the Philippine enumeration, was based on specimens cultivated in Moscow, grown from seeds secured by Mr. Porte in the Philippines (Luzon) in 1861. Regel's description is based on sterile material and from his figure, a somewhat juvenile form, for the large leaves are shown as having a fairly large lateral lobe on each side, a character that is lost in mature specimens. There is not the slightest doubt as to the identity of Warburg's species, also based on Luzon material, with the form characterized forty-three years earlier by Regel. There is some doubt in my mind as to whether or not the Indo-Chinese specimens referred here by Gagnepain actually represent the same species as the Philippine form. Its general alliance seems to be with *Fictus callosa* Willd.

FICUS PYRIFOLIA Burm. f. Fl. Ind. 226. 1768 = ***Pyrus pyrifolia*** (Burm. f.) Nakai, Bot. Mag. Tokyo 40: 564. 1926; Rehd. Man. Cult Trees Shrubs ed. 2, 404. 1940.

This reduction was made on the basis of an examination of Burman's specimens in the Delessert herbarium at Geneva; there are three sheets, all sterile, from the vicinity of Nagasaki, collected by Kleinhof; these, according to Nakai, represent the ordinary Japanese sand pear, which by various authors has been placed under *P. sinensis* auctt., *P. serotina* Rehd., and *P. montana* Nakai. Nakai attempted to define a number of minor forms of this cultigen, but no botanist has, as yet, clarified its relationships with the Chinese forms of the sand pear. In my treatment of Burman's species, Philipp. Jour. Sci. 19: 346. 1921, working solely from Burman's descriptions, I suggested that *Ficus pyrifolia* Burm. f. might prove to be the same as *Ficus erecta* Thunb., the type of which was from Japan, but this is an error. In recent years the Burman name has been attached to some Chinese collections of *Ficus erecta* Thunb.

URTICACEAE

Laportea peltata Gaudich. Freyc. Voy. Bot. 498. 1830, *nomen nudum*, et ex Decaisne, Herb. Timor. Descr. 162. 1835, *descr.*; Wedd. Arch. Mus. Hist. Nat. 9: 126. 1856 (Monog. Urt. 126), et in DC. Prodr. 16(1): 80. 1869, cum syn.; J. J. Sm. ex Koord. & Val. Meded. Dep. Landb. 10: 678. 1910 (Bijdr. Boomsoort. Java 12: 678); Koord. & Val. Atlas Baumart. Java 4: fig. 796. 1918.

Urtica peltata Blume, Bidjr. 496. 1825.

MINDANAO: Cotabato. Nutol, *Bur. Sci.* 84935, 84941, Ramos & Edano, March, 1932, a tree 8 m. high in rather dry forests at low altitudes. Java, Timor, and probably in other parts of the Malay Archipelago; new to the Philippines.

Both of the above cited specimens agree very closely with authentically named Javan specimens collected by Koorders, one having been distributed as representing the very different *Laportea crassifolia* C. B. Rob., and the other as *L. mindanaensis* Warb. It seems to be apparent that Gaudichaud did not know of the published description of *Urtica peltata* Blume, Bijdr. 496. 1825, for his original publication of the accepted binomial was simply a *nomen nudum* and a new name for *Urtica atrox* Leschen., also a *nomen nudum*. Therefore the authority should not be cited as "(Blume) Gaudichaud," but merely as Gaudichaud. The first description of the species under *Laportea* was that prepared by Decaisne, and he also cited only *Urtica atrox* Lesch. as a synonym. Weddell in 1856 first, and apparently correctly, associated Blume's earlier name with that so casually published by Gaudichaud and later validated by Decaisne.

Laportea elliptica sp. nov.

Laportea peltata sensu Merr. Univ. Calif. Publ. Bot. 15: 50. 1929, non Gaudich.

Species *L. peltatae* Gaudich. affinis, differt foliis majoribus, ellipticis, haud molliter pubescentibus sed subscaberulis et secus costam nervosque pilos urentis numerosos ferentibus, nervis primariis utrinque circiter 15. Arbor, trunco 30–45 cm. diametro, ramulis ultimis plus minusve incrassatis, siccis circiter 8 mm. diametro, pubescentibus, cicatricibus ad 8 mm. diametro notatis, partibus junioribus dense subadpresse hirsutis; foliis longe (8–13 cm.) petiolatis, perspicue peltatis, basi late rotundatis, ellipticis vel subobovato-ellipticis, chartaceis, 15–30 cm. longis, 11–15 cm. latis, apice breviter acuminatis, margine breviter dentatis vel denticulatis, dentibus inter se 1.5–3 mm. distantibus, siccis olivaceis, supra minute albido-verruculosis, secus costam pubescentibus et pilos urentis ferentibus, subtus scabridulis, paullo pallidioribus et nervis reticulisque exceptis glabris vel subglabris; nervis primariis utrinque circiter 15, perspicuis, subtus elevatis, curvato-patulis, secus marginem arcuato-anastomosantibus, reticulis distinctis, elevatis et cum costa nervisque plus minusve pubescentibus et pilos brevis numerosos urentis ferentibus; inflorescentiis longis, laxis, paniculatis, usque ad 45 cm. longis, plus minusve pubescentibus et pilis

numerosis urentibus instructis, ramis primariis 4–8 cm. longis; floribus ♀ sessilibus, in ramulis ultimis brevibus flabellatim dispositis, sessilibus, capitulis 5–9-floris, calycis segmentis acuminatis, vix 0.5 mm. longis; acheniis compressis, glabris, subovatis, 2 mm. longis, acuminatis, stylis persistentibus gracilibus, ad 3 mm. longis, leviter patule hirsutis; floribus ♂ numerosis, calycis segmentis subellipticis, 1.5–2 mm. longis, filamentis 3 mm. longis.

BRITISH NORTH BORNEO: Tawao, *Elmer* 21472 (♀), 11433 (♂), October 1922 to March 1923.

When the Elmer collections were being studied at the University of California, these specimens were referred, on the basis of published descriptions only, to *Laportea peltata* Gaudich, and were reported as such; but it was then noted that they differed from Gaudichaud's species in certain striking characters. Now that it is possible to make direct comparisons with authentically named Javan specimens of the Koorders collections, it becomes evident that there is really little in common between this Bornean form and *Laportea peltata* Gaudich., except in the conspicuously peltate leaves of both. The indumentum of the two species, as well as the leaf shape and size, and the more numerous lateral nerves in the present species are very different. In Gaudichaud's species the lower surface of the leaves is very densely and softly cinereous-pubescent, the indumentum entirely covering the parenchyma; in *Laportea elliptica* the midrib, and to a limited degree the nerves, are pubescent, but these and the reticulations bear many short, stiff, stinging hairs; yet the parenchyma within the ultimate reticulations is glabrous. In the herbarium of the Arnold Arboretum the pistillate type was found under no. 21172, *Madhuca elmeri* Merr., apparently some error having been made by Mr. Elmer in completing the labels, which makes me suspect that the same situation may exist elsewhere. The correct number is 21472, for 21172 is the *Madhuca* and 21472 the *Laportea*.

LEGUMINOSAE

Crudia cauliflora sp. nov.

Arbor parva, foliis 1-foliolatis et ramulis glabris, fructibus caulinis, breviter denseque pubescentibus; ramis ramulisque teretibus, ultimis 1 mm. diametro; foliolis subcoriaceis, oblongo-ellipticis, 15–18 cm. longis, 6–7 cm. latis, basi late rotundatis, apice distincte sed obtuse acuminatis, siccis subtus brunneis, supra subolivaceis, subopacis; nervis primariis utrinque circiter 7, subtus paullo elevatis, laxis, patulis vel subpatulis, inter se 1.5–2.5 cm. distantibus, 1–1.5 cm. a margine arcuato-anastomosantibus, reticulis primariis laxis, ultimis subconfertis; petiolo cum petiolulo circiter 1 cm. longo; racemis caulinis, solitariis, vetustioribus glabris vel partibus ultimis breviter obscure pubescentibus, saltem 10 cm. longis (floribus ignotis); fructibus solitariis, compressis, oblongo-ellipticis, leviter inaequilateralibus, 8 cm. longis, 4 cm. latis, extus pallide brunneis et dense breviterque pubescentibus, seminibus 2 vel 3.

PHILIPPINE ISLANDS: Siargao: *Ramos & Pascasio*, Bur. Sci. 34921, June 1919, the only known collection. TYPE in the herbarium of the Arnold Arboretum.

This was designated many years ago by me as new in the genus *Sindora*, but was never described, probably because I later realized that it could not represent any *Sindora*, and I had hoped that flowering specimens would eventually be received. It resembles several Malaysian species, such as *Crudia bantamensis* (Hassk.) Benth., *C. beccarii* Ridl., *C. curtisii* Prain, *C. reticulata* Merr., and even *C. subsimplicifolia* Merr. From all of these it is distinguished by its simple leaves being broadly rounded at the base; and from all described species of the genus it is distinguished by its solitary cauline racemes. None of De Wit's descriptions of the 18 Malayan species which he recognized in 1950 seems to apply to this species.*

Pithecolobium splendens (Miq.) Prain, Jour. As. Soc. Bengal 66(2): 516. 1897 (Novic. Ind. 350. 1905), *Pithecolobium in nota*.

Albizzia splendens Miq. Fl. Ind. Bat. Suppl. 280. 1861.

Pithecolobium confertum Benth. Trans. Lin. Soc. 30: 577. 1875; Bak. in Hook. f. Fl. Brit. Ind. 2: 204. 1878; Prain in King, Jour. As. Soc. Bengal 66(2): 264. 1897 [Mater. Fl. Malay. Penin. 3 (no. 9): 264], op. cit. 508; Ridl. Fl. Malay Penin. 1: 661. 1922.

Malay Peninsula, Sumatra.

Prain's new binomial does not appear in Index Kewensis nor in any of its supplements to date, yet the publication of it is valid. From his own statement it is clear that he did not intend to replace Bentham's binomial by the one based on the earlier *Albizzia splendens* Miq., as he stated that it did not appear to him to be necessary or just, to rename Bentham's species because Miquel's description was based on leaf specimens only.

RUTACEAE

Glycosmis macrantha Merr. Univ. Calif. Publ. Bot. 15: 114. 1929 (April 10).

Glycosmis oliveri Stapf ex Ridl. Kew Bull. 1930: 80. 1930, syn. nov.

The types involved are *Beccari* 2595 from Sarawak, for Stapf's species, and *Elmer* 12134, 21456, 21528 from British North Borneo, on which the earlier published *G. macrantha* Merr. was based. The only reason for publishing this note is the fact that Tanaka has added annotations to some of the Elmer numbers accepting Stapf's specific name. It is unfortunate that Stapf did not publish his new species at the time he studied *Beccari* 2595, for in publishing its first description, Ridley's work was antedated nearly a year by the publication of *G. macrantha* Merr. The two species are identical.

* DE WIT, H. C. D. The genus *Crudia* Schreb. (Leguminosae) in the Malay Archipelago south of the Philippines. Bull. Jard. Bot. Buitenz. III. 18: 407-434. fig. 1-3. 1950.

MELIACEAE

***Aglaia heterobotrys* sp. nov. § *Euaglaia*.**

Species *A. shawianae* Merr. affinis, differt foliis paullo minoribus, floribus breviter sed distincte pedicellatis, sepalis oblongis. Frutex vel arbor parva, foliis stricte 1-foliolatis, ramulis teretibus, pallidis, glabris, novellis circiter 2 mm. diametro, decidue breviter stellato-pubescentibus, indumento ferrugineo; foliis oblongo-ellipticis, chartaceis, 14–20 cm. longis, 4–7.5 cm. latis, basi late acutis vel subrotundatis, apice tenuiter acuminatis, acuminibus 1.5–2.5 cm. longis, obtusis, utrinque glabris, siccis pallide olivaceis, subnitidis; nervis primariis utrinque circiter 20, utrinque distinctis, elevatis, ad marginem arcuato-anastomosantibus; petiolo cum petiolulo 2–2.5 cm. longo, glabro; inflorescentiis in axillis superioribus, breviter stellato-pubescentibus, indumento ferrugineo, inferioribus simplicibus, ad 16 cm. longis, elongatis, floribus in partibus superioribus racemose dispositis, superioribus paniculatis, ad 14 cm. longis, pedunculatis, ramis primariis inferioribus 2.5 cm. longis, superioribus gradatim brevioribus, floribus racemose dispositis, pedicellis 0.5–1 mm. longis, bracteolis anguste lanceolatis, stellato-pubescentibus, ad 1 mm. longis; sepalis liberis vel subliberis, ad 1 mm. longis, oblongis vel anguste oblongis, obtusis vel subacutis, stellato-pubescentibus, 1 mm. longis; petalis 5, glabris, liberis, oblongo-obovatis vel late oblanceolatis, obtusis, 2 mm. longis, 0.6–1 mm. latis; tubo glabro, libero, 1.8 mm. longo, antheris 5, 0.4 mm. longis, inclusis, ovario dense pubescenti.

SUMATRA: East Coast, Kota Pinang District, Si Mandi Angin on the Soengei Kanan, topographic sheet 41, southeast corner, *Rahmat Si Toroes* 4197, April–May, 1933, with the local name *kajoe pīran*.

The alliance of this species is clearly with that small group of simple-leaved species of which the Bornean *Aglaia triandra* Ridl., *A. odoardoi* Merr., *A. matthewsii* Merr., and *A. shawiana* Merr., as well as the Siamese *A. meliosmoides* Craib, are typical. It is distinguished by its vegetative and other characters, and particularly by its always racemosely arranged, shortly but distinctly pedicelled flowers. The inflorescences in the lower leaf axils are greatly elongated simple racemes, the flowers borne only along the upper 2 to 3 cm., but the uppermost inflorescence is a normal panicle.

Walsura monophylla* Elm. Leaf. Philipp. Bot. 9: 3391. 1937, *descr. angl.

Arbor 5.5 m. alta, inflorescentiis obscure pubescentibus exceptis glabra, foliis omnibus 1-foliolatis. Ramulis teretibus, glabris, lenticellatis, ultimis circiter 2 mm. diametro; foliolis oblongo-ellipticis, coriaceis, 11–28 cm. longis, 4–8 cm. latis, subtus pallidis, brevissime et acute acuminatis vel acutis, basi plerumque obtusis, nervis primariis utrinque 10–15, subpatulis, curvatis, arcuato-anastomosantibus, subtus distinctioribus; petiolo 1–2 cm.

longo; inflorescentiis terminalibus, anguste paniculatis, circiter 7 cm. longis, obscure pubescentibus, ramis primariis 1–1.5 cm. longis, patulis; floribus inter majores, flavido-albidis, circiter 4 mm. longis, 5-meris; sepalis triangulari-ovatis, acutis, obscure pubescentibus; petalis oblongis, obtusis vel subacutis, glabris, 4 mm. longis, 2 mm. latis; filamentis pubescentibus, tubo deorsum utrinque glabro; fructibus junioribus 5–8 mm. longis, breviter ellipsoideis vel subovoideis, pubescentibus.

A second Philippine collection of this species is *Ebalo 556* from Mount Langogan, near Puerto Princesa, Palawan, Feb. 23, 1940; the type is *Elmer 12903* from Brooks Point, Palawan. The above Latin description has been prepared to validate Elmer's binomial. The striking character of the species is its strictly 1-foliolate leaves, all other known species of the genus having pinnate leaves. It has long been known that *Aglaia*, another genus of the family, does contain a fair number of species with strictly simple leaves, although in the vast majority of its species the leaves are pinnate, and in all the known species of *Vavaea* the leaves are strictly simple. This reduction of pinnate leaves to simple ones in certain species of *Aglaia* is now paralleled in *Walsura*.

EUPHORBIACEAE

Aporosa cardiosperma (Gaertn.) comb. nov.

Croton cardiospermum Gaertn. Fruct. 2: 120. *pl.* 107. *fig.* [11]. 1791.

Agyneia latifolia Moon, Cat. Pl. Ceyl. 65. 1824.

Aporosa latifolia (Moon) Thwaites. Enum. Pl. Ceyl. 288. 1864; Trimen, Hand-book Fl. Ceyl. 4: 39. 1898; Pax & Hoffm. Pflanzenr. 81 (IV. 147. XV): 96. 1922.

A species known only from Ceylon. The identity of Gaertner's species with that later described as *A. latifolia* (Moon) Thwaites was determined by Hallier f., Rec. Trav. Bot. Néerl. 15: 35. 1918. According to Thwaites the native name *kebella*, cited by Gaertner, belongs with the distinctly different *Aporosa lindleyana* Baill., but the characters as described by Gaertner and the details of his figure are those of the Thwaites, not of the Baillon species.

At the end of volume two of his *De fructibus et seminibus plantarum*, Gaertner assembled under a center heading *Barbarae* nine alphabetically arranged taxa which he described and figured under their native names (Ceylon and Java), Fruct. 2: 485–488. *pl.* 180. 1791. Hallier f., op. cit., gave some attention to the identity of these, although the descriptions were manifestly not intended to represent new genera, nor are any binomials used. They are merely casual names for those fruits that Gaertner had which he could not refer to any described genus. A very few of these names have appeared in taxonomic literature as if genera were intended, and in two cases binomials are involved, although the latter were not originated by Gaertner. Hence, the identification of these old Gaertner taxa in terms of the binomial system is of only slight academic interest, as they scarcely bear on problems of nomenclature. The entries are as follows:

"*Balangué. E. madagasc.*"

This is the whole basis of *Balangué gaertneri* DC. Prodr. 8: 316. 1844. It is possibly some rhamnaceous plant.

"*Cucumeroides. Ex Japonia.*" = *Trichosanthes*.

"*Edokke zeylonens.*" = *Chaetocarpus castanocarpus* Thwaites.

"*Giek zeylonens.*" = *Odina wodier* Roxb. = *Lannea coromandelica* (Houtt.) Merrill, Jour. Arnold Arb. 19: 353. 1938, *cum syn.*

"*Zoon zelonens.*" = *Schleichera oleosa* (Lour.) Oken, Allgem. Naturgesch. 3(2): 1341. 1841; Merr. Interpret. Herb. Amb. 337. 1917, Jour. Arnold Arb. 31: 284. 1950. (*Schleichera trijuga* Willd.).

This in earlier years, was referred to the menispermaceous *Pachygone ovata* (Poir.) Miers, and appears as a synonym of that species in the latest monographic treatment of the family, Diels, Pflanzenz. 46(IV. 94): 343. 1910, where it does not belong. The binomial *K. zeylanicus* is currently credited to Gaertner, but he did not originate it. The earliest reference to it that I have located is in the synonymy of Miers' species, Hooker f. & Thomson in Hook. f., Fl. Ind. 1: 105. 1872.

"*More zeylonens.*" = *Euphorbia longana* Lam.

"*Pite-heddiya javan.*" = ?

"*Terme javan.*" = *Acronychia*?

"*Wal-tiedde & Keipisan Zeylonens.*" = ?

Apparently some menispermaceous plant, perhaps *Tiliacora*, is represented.

ANACARDIACEAE

Parishia maingayi Hook. f. Fl. Brit. Ind. 2: 30. 1876; King, Jour. As. Soc. Bengal 65(2): 493. 1896 (Mater. Fl. Malay. Penin. 2: 779); Ridl. Fl. Malay Penin. 1: 535. 1922.

Parishia elmeri Merr. Univ. Calif. Publ. Bot. 15: 168. 1929, *syn. nov.*

I am now convinced that *Parishia elmeri* Merr. (1929), type from British North Borneo (Elmer 21662) belongs with Hooker's species and it is accordingly reduced to the latter. This gives its range as the Malay Peninsula, Sumatra, Riouw, and Borneo, a very natural one. The Sumatran and Riouw specimens that I have seen are sterile.

Parishia malabog Merr. Philipp. Jour. Sci. 7: Bot. 281. 1912, Enum. Philipp. Fl. Pl. 2: 472. 1928.

Spondias romblonensis Elm. Leaf. Philipp. Bot. 10: 3683. 1939, *descr. angl., syn. nov.*

The type of Elmer's species, now reduced, is a staminate specimen, his number 12164 from Romblon. See the note at the end of my original description of 1912. Luzon (Tayabas), Mindoro, Ticao, Masbate, Sibuyan, Tablas, Romblon, Cebu, and Sibutu Islands. Endemic.

CELASTRACEAE

Celastrus paniculatus Willd. Sp. Pl. 1: 1125. 1798.

Alsodeia glabra Burgersdyk in Miquel, Pl. Jungh. 122. 1852; Miq. Fl. Ind.

Bat. 1(2): 116. 1858; Oudem. Arch. Néerl. 2: 199. *pl.* 9. 1867, *syn. nov.*

Rinorea glabra O. Kuntze, Rev. Gen. Pl. 1: 42. 1891, *syn. nov.*

The type of *Alsodeia glabra* Burgersdyk, a fruiting specimen, was collected in Sumatra by Junghuhn. I had suspected from Oudemans's excellent illustration, because of the terminal panicle (in fruit) and other characters, that a *Celastrus* was represented and not a representative of the violaceous *Alsodeia* = *Rinorea*. Accordingly, while in Leiden I looked up the type and found that Hallier had already made the transfer to *Celastrus* in the herbarium but that he considered that a valid species of that genus was represented: I can find no record of his having published this conclusion. To me the Junghuhn specimen represents a form of the widely distributed *Celastrus paniculatus* Willd., type from India, the species, as currently interpreted, extending to Ceylon, Burma, Siam, Indo-China, southeastern China, the Philippines, Malay Peninsula (and now Sumatra), Java, and Timor. I have seen no specimens from Borneo, although it is to be expected there, as well as in Celebes and the Moluccas. Koorders, who in 1909 studied the type of *Flüggea* ? *serrata* Miq. (1858) from Java, correctly reduced that species to *Celastrus*, and further to *C. paniculatus* Willd. Other synonyms currently placed here are: *Celastrus alnifolius* D. Don, *C. dependens* Wall., *C. multiflorus* Roxb., *C. rothianus* Roem. & Schult., *C. metzianus* Turcz., *C. polybotrys* Turcz., *Ceanothus paniculatus* Roth., *Scutia paniculata* G. Don, and *Diosma serrata* Blanco.

Kurrimia robusta (Roxb.) Kurz. Jour. As. Soc. Bengal. 39(2): 73. 1870;
Pitard in Lecomte, Fl. Gén. Indo-Chine 1: 893. 1912.

Celastrus robustus Roxb. Fl. Ind. 2: 395. 1824.

Bhesa moja Ham. ex Arn. Edinb. New Philos. Jour. 16: 315. 1834.

Rhesa moja Walp. Repert. 1: 538. 1842.

Kurrimia pulcherrima Wall. List no. 4334. 1830, *nom.*; Laws. in Hook. f. Fl. Brit. Ind. 1: 622. 1875, *descr.*

Nothocnestis sumatrana Miq. Fl. Ind. Bat. Suppl. 531. 1862.

Sarcosperma tonkinense H. Lecomte, Bull. Mus. Hist. Nat. Paris 24: 534. 1918, Fl. Gén. Indo-Chine 3: 914. 1930, *syn. nov.*

In their critical treatment of the Sarcospermataceae, Lam and Varosieau, *Plumetia* 3: 198. 1939, who had seen Lecomte's type, a fruiting specimen, correctly eliminated *Sarcosperma tonkinense* H. Lecomte from the genus and family and concluded that it was probably not even a sapotaceous plant; no identification of it was suggested. While in Paris in August 1950, I examined the type and at once the problem resolved itself. Manifestly Lecomte's type, *Bon* 3974, represents a species of the celastraceous *Kurrimia*, not a *Sarcosperma*. Direct comparisons then made showed that it was a fruiting specimen of the rather common and widely

distributed *Kurrimia robusta* (Roxb.) Kurz, which extends from Khasia and Silhet to Burma, Siam, and Indo-China southward to Singapore and Sumatra. I think that *Nothocnestis sumatrana* Miq. Fl. Ind. Bat. Suppl. 531. 1862, is correctly placed as a synonym of Roxburgh's species, for although I have not seen its type I take Netherl. Ind. For. Serv. 31688, 32124 from Palembang, Sumatra, the type locality of Miquel's monotypic genus, to represent it, and I refer these two modern collections to *Kurrimia robusta* (Roxb.) Kurz.

RHAMNACEAE

Ventilago gamblei nom. nov.

Ventilago lanceolata Gamble, Kew Bull. 1916: 134. 1916; Alston in Trimen Hand-book Fl. Ceyl. Suppl. 49. 1931, non Merr. (1915).

A new name is needed for this species of southern India and Ceylon, as the one selected by Gamble in 1916 had been used by me for a different Philippine species one year earlier.

ELAEOCARPACEAE

Elaeocarpus tectorius (Lour.) Poir. in Lam. Encycl. Suppl. 2: 704. 1812, excl. fruct.; Merr. Trans. Am. Philos. Soc. II. 24(2): 256. 1935.

Craspedum tectorium Lour. Fl. Cochinch. 336. 1790, ed. Willd. 411. 1793.

Dicera craspedum J. F. Gmel. ex DC. Prodr. 1: 520. 1824.

Elaeocarpus robustus sensu Merr. Jour. Arnold Arb. 32: 189. 1951, excl. syn. plur., non Roxb. § Chascanthus.

This is an endemic species of Indo-China erroneously placed as the equivalent of *Elaeocarpus robustus* Roxb., the type of which was from Silhet, India. In the rather extensive synonymy cited by me in 1951 only *Craspedum tectorium* Lour. and *Dicera craspedum* J. F. Gmel. actually belong with the Loureiro *Elaeocarpus* species above cited. Loureiro's genus and species were based on specimens from the vicinity of Hue, Indo-China. Clemens 3688 (in flower) and 4156 (in fruit) were collected near Tourane, which is about 100 kilometers south of Hue. Clearly most of the Cochinese species characterized by Loureiro were observed in the vicinity of Hue, where he lived for many years. Both the Clemens' numbers are in the Paris and the University of California herbaria, and the first is also at Kew and the Arnold Arboretum. In 1951 I very critically compared the Kew specimen with the Loureiro one at the British Museum, and surely a single species is represented. Clemens 3688 is with mature flowers; the Loureiro specimen has very immature buds.

The Loureiro original description is ample and well prepared. He unfortunately "guessed" at the fruit characters in his generic description of *Craspedum*, and for this reason Corner illogically refused to recognize *Craspedum tectorium* Lour. as worthy of consideration. I disagreed with

him then as I do now, for all one has to do is to exclude the description of the fruit in Loureiro's generic account of *Craspedum*; the specific description was wholly based on a flowering specimen.

Dr. Gagnepain in 1943 (Not. Syst. 11: 1-14) increased the number of Indo-Chinese species of *Elaeocarpus* by describing twelve new ones. He did not indicate the sections in accordance with Schlechter's scheme of classification, but no less than eight of them belong in *Chascanthus* by the indicated number of ovary cells (3) and the number of ovules in each cell (2).

This note is prepared to correct my error of 1951 when I misinterpreted Loureiro's species by reducing it to *Elaeocarpus robustus* Roxb. I add brief descriptive data based on the Loureiro specimen in the British Museum and *Clemens* 3688, 4156 from near the type locality. Dr. Gagnepain left the two Clemens collections in the Paris herbarium without comment under the binomial *Elaeocarpus tectorius* (Lour.) Poir. which I assigned to them when the identifications were made by me and the sets of duplicates were distributed in 1927-28. I can only assume he approved of my identifications. I am indebted to Dr. Tardieu-Blot for checking the specimens.

Leaves nearly or quite glabrous, 7-13 cm. long and 3-5.5 cm. wide; lateral nerves 7 to 9 or 10 pairs; petiole 2-3.5 cm. long; flowers about 1 cm. in diameter, the petals 20-30-lacinate; ovary hairy, 3-celled, cells 2-ovulate. Fruit ellipsoid, sharply apiculate, practically glabrous, the bony endocarp very rugose. A photograph of the Loureiro specimens, a carbon rubbing of a full-grown leaf, and extensive notes are in the Arnold Arboretum herbarium; this was a second and later collection by Loureiro, sent by him as representing his species. The specimen is not the actual type.

DILLENIACEAE

Saurauia costata Reinw. ex de Vriese, Pl. Ind. Bat. Or. 56. 1856.

Saurauia warburgii Koord. Meded. Lands Plant. 19: 354, 644. 1898, Suppl. Fl. Celeb. 2: pl. 80. 1922 (poor), 3: 39. 1922, syn. nov.

Reinwardt's species was based on material collected by him in October 1821 on Mount Sempo, Celebes, there being three sheets of this collection in the Rijksherbarium, Leiden. It is suspected that Koorders did not see these specimens, for otherwise he would scarcely have proposed *S. warburgii* Koord. as new in 1898. The latter was based on *Koorders* 18954, 19283, from Minahassa Province, northeastern Celebes. The several sheets representing the two supposedly different species are so similar that all might have been taken off the same plant or stand of plants.

De Vriese, in publishing Reinwardt's description, noted that this Celebes form resembled a Philippine collection, *Cuming* 455, which he described, l.c., as *Saurauia exasperata* De Vr.; this is, however, *Saurauia latibractea* Choisy (1854) as I understand that species, one that clearly is not closely allied to *S. costata* Reinw. Koorders stated that his new species was allied

to the Philippine *Saurauia elegans* (Choisy) F.-Vill. (*S. rugosa* Turcz.), and Stapf had noted on one of the Reinwardt sheets that it was "very near *S. rugosa* Turcz." In the latter species, which occurs in most provinces in Luzon and in Mindoro, the lax, long-peduncled, many-flowered inflorescences are up to 16 cm. long and 10 to 12 cm. wide, while its smaller leaves are, as Koorders noted, rounded, not cordate, at the base. He described the inflorescences of *E. warburgii* Koord. as only 2.5 cm. long. Although the vegetative characters of the two species are suggestively similar, I do not think that they are closely allied.

Saurauia lanceolata DC. Mém. Soc. Phys. Hist. Nat. Genève 1: 421. 1821, quoad descr., excl. pl. 4; DC. Prodr. 1: 526. 1824; De Vriese, Pl. Ind. Bat. Or. 39. 1856.

This is a very curious case. It is suspected that most authors have interpreted De Candolle's species from his distinctly good plate. His technical description was based wholly on a Javan specimen, *Leschenault* 643, the type being in the Paris herbarium. An excellent photograph of this type, kindly supplied by Madame Tardieu-Blot, is before me, including even the supplementary sheet with sketches of the flower and dissection notes. As will be seen from the photograph, the *Leschenault* specimen (no. 643) has only slightly developed inflorescences. This type should be compared critically with that of *Saurauia micrantha* Blume from Mt. Gede. Although no exact locality in Java is given for *S. lanceolata* DC., it would have to be from a readily accessible place, such as Mt. Gede.

The strange thing is how De Candolle's plate became associated with the Javan species. Zollinger, Syst. Verzeichn. 148. 1854, noted the great similarity of illustration to the South American *S. ruiziana* Steud., stating: "*S. lanceolata* DC. Mem. t. IV tam similis est *S. Ruizianae* Steud. (Ap[ateria] lanceolata D.C) ut nullomodo distincta videatur quamvis petalis basi coalitis. An de patria error quisdam in herbario Parisii adfuit?" Madame Tardieu-Blot says: "Le type est glabre (photo) et correspond à la description. Au contraire, la figure (Pl. IV) est très différente (value) et cadre très bien avec *S. Ruiziana*." De Candolle's specific epithet has priority over any other designating a plant with which this type can be matched.

GUTTIFERAE

Calophyllum rotundifolium Ridl. Jour. Fed. Malay States Mus. 5: 22. 1914; Fl. Mal. Penin. 1: 188. 1922.

British North Borneo, Mount. Kinabalu, *Clemens* 30984, 31428, 35038, 40705, 50316. The altitudinal range is indicated on two labels as 4,000 and 5,000 ft. I cannot distinguish this strongly marked species from Ridley's type at Kew. The sessile, broadly cordate, suborbicular to broadly ovate leaves vary in length from 2 to 7 cm., their apices rounded or very broadly rounded occasionally slightly retuse. Malay Peninsula (Selangor), alt. 5000 ft. New to Borneo.

VIOLACEAE

Rinorea lanceolata (Roxb.) O. Kuntze, Rev. Gen. Pl. 1: 42. 1891.

Vareca lanceolata Roxb. Fl. Ind. 2: 446. 1824, ed. 2, 1: 648. 1832.

Celastrus pauciflora Wall. in Roxb. Fl. Ind. 2: 400. 1824.

Pentaloba lanceolata Wall. List no. 4023. 1830, *nom. nud.*

Pittosporum ? serrulatum Jack ex Griff. Calcutta Jour. Nat. Hist. 4: 195. 1843, *syn. nov.*

Alsodeia lanceolata Oudem. Arch. Néerl. 2: 196. *pl.* 6. 1867; Hook. f. Fl. Brit.

Ind. 1: 188. 1872; King & Gamble, Jour. As. Soc. Bengal 58 (2): 404. 1889

(Mater. Fl. Malay. Penin. 1: 48); Ridl. Fl. Malay Penin. 1: 131. 1922.

For a rather sharply characterized species known only from Penang Island, this has accumulated a considerable synonymy. My attention was called to it through an attempt to place the generally ignored binomials *Pittosporum ? serrulatum* Jack and *Celastrus pauciflora* Wall., both based on Penang material. Jack sent a copy of his description to Wallich, who realized at once that no *Pittosporum* was represented, and, as he says he had no specimens from Jack, he apparently surmised from the description that *Celastrus* might be the proper place for it and so described it as his own species, although stating that the description was from Jack. Griffith, who edited the Calcutta reprint of Jack's plant descriptions in 1843, says that his data were from Jack's MS., yet these are the same as those published under *Celastrus pauciflora* Wall. It is suspected that Jack did send a specimen to Wallich which the latter failed to associate with Jack's manuscript description. Under *Vareca lanceolata* Roxb. Flora Ind. 2: 446. 1824. Wallich states: "I have specimens belonging probably to this plant, which were collected at Pinang by W. Jack, who in a Mss. note says: 'I am at a loss what to make of this shrub. I thought it might be a *Vareca* (according to Roxburgh) but the *capsule* is one-celled, *three-valved*, with parietal placentae.'" There is a specimen of Wallich 4023, type collection of *Pentaloba lanceolata* Wall. which, as far as the record goes, was not based on *Vareca lanceolata* Roxb., and two modern collections of the species from Penang in the herbarium of the Arnold Arboretum. As far as the two somewhat generalized descriptions of Jack and of Wallich are concerned, they agree in all respects with the characters of *Rinorea lanceolata* (Roxb.) O. Kuntze, the type of which was from Penang.

Rinorea semigyrata (Turcz.) J. J. Sm. in Koord. & Val. Meded. Dep. Landbouw 18: 73. 1914 (Bijdr. Boomsoort. Java 13: 73).

Pentaloba semigyrata Turcz. Bull. Soc. Nat. Moscou 27 (2): 342. 1854.

Alsodeia disticha Zoll. ex Teysm. & Binn. Cat. Hort. Bogor. 183. 1866, *nom.*, et in Miq. Ann. Mus. Bot. Lugd.-Bat. 4: 216. 1869, *nom.*, *syn. nov.*

Alsodeia semigyrata Turcz. ex Jacks. Ind. Kew. 1: 93. 1893.

Alsodeia paradoxa Blume ex Oudem. Arch. Néerl. 2: 204. *pl.* 15. 1867, et in Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 71. 1867.

Rinorea paradoxa J. J. Sm. in Koord. & Val. op. cit. 67; Van Ooststr. in Backer Beknopte Fl. Java 4a (1): Fam. 48. 3. 1942.

Turczaninow's specific name is apparently the oldest valid one for this rare, or perhaps even extinct Javan species. His type was *Zollinger 2979*, and a duplicate of this collection is in the herbarium of the Arnold Arboretum, acquired in 1941 from the Boston Museum of Natural History, having originally been in the private herbarium of John Amory Lowell. The original description is short and unsatisfactory, leading J. J. Smith, who reproduced it in 1914, to think that perhaps some genus other than *Rinorea* was represented; yet he actually effected the transfer of the specific epithet to *Rinorea*. Van Ooststroom in 1942 apparently saw only the Blume material at Leiden, there being at least four sheets labeled by Blume as *Alsodeia paradoxa*; these specimens came from the Salak and Boerangrang Mountains, western Java. The region has been very intensively explored in the past century. He noted that the species had apparently not been collected since Blume's time. I cannot distinguish *Zollinger 2979* from these Blume specimens, its label merely indicating that it was collected in Java. It also bears an unpublished Zollinger binomial in *Imhofia*. This leads me to reduce, without question, the *nomen nudum*, *Alsodeia disticha* Zoll., as this specific epithet is the one that appears on our Zollinger specimen sub *Imhofia*. It is suspected that at first Zollinger thought that he had a representative of a new genus and then found that the generic name originally assigned to his number 2979 was a preoccupied one. Teijsmann and Binnendijk, who first printed the Zollinger binomial, merely indicate the species as being from "Ind. or." Some of the higher numbers of the Zollinger collection distributed under Java labels were actually from Sumatra.

I note that although *Rinorea semigyrate* J. J. Sm. was legitimately published in 1914, it was overlooked by the compilers to the supplements to Index Kewensis. Further I note that the binomial *Alsodeia semigyrate* was not actually published by Turczaninow, Bull. Soc. Nat. Mosc. 36(1): 559. 1863, as currently accepted. All that he stated was that his three species of *Pentaloba* (*P. corylifolia*, *P. fasciculata*, and *P. semigyrate*) represented species of *Alsodeia*, but he made no actual transfers.

LYTHRACEAE

Lagerstroemia speciosa (Linn.) Pers. (*L. flos-reginae* Retz.)

I have always been impressed by the apparent reluctance of certain taxonomists to accept changes in the accepted names of plants on the basis of the priority rule, no matter what the evidence is, and no matter what botanist upset the use of a generally accepted binomial strictly in accordance with the Code. A case in point is the very common and widely distributed *Lagerstroemia speciosa* (Linn.) Pers. versus the later *L. flos-reginae* Retz. When Koehne's monograph of the Lythraceae appeared (Pflanzenreich 17 (IV. 216): 1-326. fig. 1-59. 1903) he correctly accepted the Linnaean specific epithet, and as he was known to be a very critical worker, I did not hesitate to accept his conclusions. The species

extends from northern India southward and eastward through Malaysia to New Guinea and northeastern Australia, and is, I suppose, one of the most frequently collected of the arborescent species because it is so common and so conspicuous, when in flower, in most parts of its very wide range. From Koehne's references it is manifest that he had checked the first publication of the name-bringing binomial. I was therefore somewhat surprised to note that Mr. Corner, Gard. Bull. Straits Settl. 10; 272. 1939, rather curtly rejected *L. speciosa* (Linn.) Pers. and accepted the later *L. flos-reginae* Retz. He rested his case on King's statement, Jour. As. Soc. Bengal 67(2): 9. 1898, and manifestly did not check the original documents. King's whole argument is merely that the acceptance of the Linnaean specific name of 1771 was inadmissible, as "he describes *M[unchausia]* *speciosa* as a *shrub* [which is true, as Linnaeus does say "arbuscula": he had a plant grown in a greenhouse in Germany], whereas this plant [*L. flos-reginae* Retz.] is a large tree; moreover the rest of the description would apply to various other species of *Lagerstroemia*." The last part of this statement is true, for the Linnaean description of 1771 is very short and very unsatisfactory. Yet the species is by no means always a large tree: I have seen immature plants in full flower on Luzon that were not more than 2 m. high. But what Koehne did not overlook, as did both King and Corner, is that the original description of *Munchausia speciosa* Linn. was published in Muenchhausen's *Der Hausvater* 5: 357. pl. 2. 1770. This description is not only an ample one, but it is accompanied by a really excellent plate: and the plant described and illustrated is in all respects *L. flos-reginae* Retz. = *L. speciosa* (L.) Pers. Yet Corner would maintain Retz's specific name even at this late date. The description, according to Muenchhausen's own statement, was prepared by Linnaeus, in spite of the fact that a year later Linnaeus credited it to Muenchhausen. The specimens on which the description and the illustration were based were from a plant cultivated in the Botanical Garden at Goettingen, the source of it being stated as Java, and at the same time the common Javanese name *boengoes* was listed, the modern *boengoer* which is widely used in western Java. Muenchhausen said Java and China, — Linnaeus only China.

Turning to the Linnaean herbarium, a set of photographs of all the sheets being available at the Arnold Arboretum, there are three sheets in the *Munchausia* cover, none of them actually named by Linnaeus; but two of these are manifestly this very common *Lagerstroemia*, and for the most part the plate illustrating the species might have been drawn from these; and in Linnaeus' handwriting on one of these is the name *boengoes*.

We who attempt to apply the approved rules of nomenclature in the determination of the oldest valid specific name for this or that species are always subject to criticism on the part of those who apparently abhor changes in names of well-known species. Generally speaking it will probably be admitted that those who make changes try to do the best that they can with the data which are available to them. We all make mistakes, but that is no reason why we should be tacitly condemned merely because

we do, on occasion, correctly interpret a Linnaean type. There is no approved method whereby the oldest specific name can be abandoned in this case.

MYRSINACEAE

Ardisia oligocarpa nom. nov.

Ardisia oligantha Elm. Leaf. Philipp. Bot. 4: 1496. 1912; Merr. Enum. Philipp. Fl. Pl. 4: 260. 1923, non Baker (1885), nec Mez (1902).

The type and only known collection is *Elmer 12310* from Sibuyan, the flowers unknown. The species belongs in the subgenus *Pyrgus* in the alliance with *Ardisia perrottetiana* A. DC. and *A. serrata* Pers., but has much smaller, differently shaped, entire or nearly entire leaves, and short infructescences with very few fruits and apparently with very few flowers.

Ardisia diversifolia Koord. & Val. Meded. Lands Plant. 33: 249. 1900 (Bijdr. 5: 249).

Ardisia oligantha Mez, Pflanzenr. 9 (IV. 246): 134. 1902, **syn. nov.**

Ardisia javanica A. DC. var. *oligantha* Blume ex Scheff. Comm. Myrsin. Archipel. Ind. 74. 1867.

The Mez binomial was based on a single Reinwardt specimen from Mount Salatta, Java, in the Rijksherbarium, Leiden. It is not accounted for in Backer's recent treatment of the Myrsinaceae of Java, Beknopte Fl. Jav. VIIB Myrsinaceae 1-20. 1948. I do not see how this can be distinguished from the Koorders and Valeton species, of which Mez saw no specimens. He placed the latter next to his new one, stating "ex descriptione sequenti [*A. oligantha* Mez] peraffinis"; and in his key to the species on page 73 he apparently could discover no characters by which the two could be distinguished, merely inserting the Javan *A. diversifolia* Koord. & Val. between *A. verrucosa* Presl, a Philippine species, and *A. oligantha* Mez of Java, but indicating no separating characters.

Ardisia taytayensis nom. nov.

Ardisia pachyphylla Merr. Philipp. Jour. Sci. 12: Bot. 157. 1917, Enum. Philipp. Fl. Pl. 3: 261. 1923, non Dunn (1912).

A species known from Palawan and Balabac, *Merrill 9188, 9216, Escritor* Bur. Sci. 21613.

Discocalyx papuana (S. Moore) comb. nov.

Embelia papuana S. Moore, Trans. Linn. Soc. Bot. II. 9: 106. 1916.

The type and only known collection is a Boden-Kloss specimen, Wollaston expedition from Camp VIb Mt. Carstensz, New Guinea, alt. about 1200 m. This is clearly a small erect shrub, not scandent as are all representatives of *Embelia*; Moore did not indicate its habit, and there are no notes.

***Embelia cotinoides* (S. Moore) comb. nov.**

Maesa cotinoides S. Moore, Trans. Linn. Soc. Bot. II. 9: 103. 1916.

The type of this in the herbarium of the British Museum is an excellent specimen collected by C. Boden-Kloss at Camp VIa Mt. Carstensz alt. 940 m. on the Wollaston expedition to New Guinea, 1912-13. It is in all respects an *Embelia* of the subgenus *Euembelia* in the general alliance with *Embelia sarasinorum* Mez of Celebes and the more widely distributed Malayan *E. coriacea* Wall. but is very distinct from both.

EMBELIA ? LUCIDA Wall. List no. 2315. 1830, *nom. nud.*, et ex A. DC. in Trans. Linn. Soc. 17: 134. 1834, *descr.*, Prodr. 8: 87. 1844 = **Antidesma coriaceum** Tul. Ann. Sci. Nat. Bot. III. 15: 204. 1851, non *Antidesma lucidum* Merr. (1906).

When a species is described as new but placed not only in the wrong genus but in a family remote from the one to which it belongs, it is sometimes worth while to prepare a record when a correct reduction can be made. Although Mez saw the holotype in the De Candolle herbarium, he was unable to place the species, merely indicating that it did not belong in the Myrsinaceae. At my request Mr. Burkill examined *Wallich 2315* at Kew, the type collection from Singapore, and reported to me that, although no flowers are left on the specimen (it was apparently pistillate, judging from De Candolle's description), *Embelia* ? *lucida* Wall. is safely the same as *Antidesma coriaceum* Tul. Other synonyms are *Antidesma fallax*, Muell.-Arg. (1865) and *A. pachyphyllum* Merr. (1916). Wallich's name cannot be used in *Antidesma* because of the different *Antidesma lucidum* Merr. (1906). Penang, Malay Peninsula, Singapore, Borneo; planted at Bogor, Java, fide Pax & Hoffmann.

***Maesa megaphylla* Merr.** Philipp. Jour. Sci. 12: Bot. 158. 1917, Enum. Philipp. Fl. Pl. 3: 255. 1923.

Maesa lobuligera Mez, Repert. Sp. Nov. 16: 310. 1920.

Maesa megalobotrys Merr. op. cit. 20: 422. 1922, *syn. nov.*

Maesa celebica Koord. ex Koord.-Schum. Syst. Verzeich. Herb. Koord. 3: 100. 1914, *nom. nud.*, *syn. nov.*

The type of *Maesa megaphylla* Merr. was *Wenzel 1510* from Leyte, that of *M. lobuligera* Mez, *Foxworthy* Bur. Sci. 727 from Palawan, that of *M. megalobotrys* Merr., *Merrill 9176* from Palawan, and that of *M. celebica* Koord., *Koorders 18174* from Minahassa, northeastern Celebes. Had Koorders published a description of the latter, then his specific name would be the accepted one for this rather strongly marked species. The specimen of *Koorders 18174* at the Rijksherbarium, which I have seen, is fragmentary and sterile, consisting of a branchlet and two large glabrous detached leaves, these about 15 to 18 cm. long and 9 to 12 cm. wide. It is suspected that the reason why Koorders published no description is that he had only sterile material. In such a critical genus as *Maesa*, where

species are often distinguished by very slight characters, some might hesitate in reducing a binomial to synonymy where only vegetative parts are known, but the agreements in this case are so close, and the flora of northern Celebes is so similar to that of the Philippines, that I do not hesitate to place Koorders' name in synonymy. It is perhaps unreasonable to discuss the reduction of a mere *nomen nudum* in detail. Actual specimens now available to me are: Leyte, Wenzel 1275, 1510, 1627 (two of these distributed under another binomial invalidated by *Maesa platyphylla* Elm.); Bohol, Ramos Bur. Sci. 43324; Dinagat, Ramos & Convocar Bur. Sci. 84657; Celebes, Minahassa, Koorders 18174. No specimen of Merrill 9176 is at present available to me. From the description I had surmised that *Maesa megalobotrys* Merr. was not distinct from *M. megalophylla* Merr., and Dr. E. H. Walker, after examining an isotype of the former in the U. S. National Herbarium, confirms this reduction of it. It is also recorded from Palawan and from Mindanao.

OLEACEAE

Ligustrum robustum (Roxb.) Blume, Mus. Bot. Lugd.-Bat. 1: 313. 1850; Mansf. Bot. Jahrb. 59: Beibl. 132: 44. 1924, *cum syn.*

Phillyrea robusta Roxb. Fl. Ind. 1: 101. 1820.

Olea puberula Ridl. Jour. Straits Br. Roy. As. Soc. 59: 128. 1911, Fl. Malay Penin. 2: 318. 1923, *syn. nov.*

In checking certain types of *Olea* at Kew in 1950 I noted a duplicate type of *Olea puberula* Ridl., i.e., Ridley 15223 from Perlis, Malay Peninsula, and although the specimen is a poorly prepared one, manifestly *Ligustrum* rather than *Olea* is represented; this might be suspected from Ridley's description of his species as having terminal panicles. The note made at the time is to the effect that it was apparently a form of *Ligustrum robustum* (Roxb.) Blume with inflorescences narrower than in the typical form. As Roxburgh's species is currently interpreted, it extends from Nepaul, Silhet, Assam, and Bengal to Chittagong, Burma, Siam, Indo-China, and Sumatra, so that this extension of range to the Malay Peninsula is not surprising. For the present I prefer thus to dispose of Ridley's species, rather than by transferring his specific name to *Ligustrum*; in any case this is the first record of the genus *Ligustrum* for the Malay Peninsula.

Linociera pachyphylla sp. nov.

Arbor glabra, inflorescentiis parcissime pubescentibus exceptis, ramulis ultimis subpallidis, teretibus, consperse lenticellatis, 3–4 mm. diametro, nodis superioribus plus minusve compressis; foliis crasse coriaceis, rigidis, siccis utrinque brunneis vel castaneis, subconcoloribus vel subtus paullo pallidioribus, supra nitidis, oblongis vel oblongo-ellipticis, 18–27 cm. longis, 7–9 cm. latis, breviter subobtuse acuminatis, basi late acutis, nervis primariis utrinque 10–12, supra impressis, subtus elevatis, perspicuis, circiter ad marginem valde curvatis, fere anastomosantibus, reticulis pri-

mariis laxis, obscuris, secundariis obsoletis; petiolo crasso, 1.5–2 cm. longo; inflorescentiis axillaribus, solitariis, breviter pedunculatis vel e basi ramosis, 6–7 cm. longis, ramis primariis patulis vel adscendentibus; floribus numerosis, breviter pedicellatis, bracteis inferioribus crassissime coriaceis, ovatis, concavis, circiter 3 mm. longis, superioribus brevioribus; petalis fere liberis, loriformibus, obtusis, 5 mm. longis, basi circiter 1.5 mm. latis, sursum vix 1 mm. latis; antheris 1.1 mm. longis.

BORNEO: Sarawak: *Native collector* 584, notes lost.

This was distributed as representing *Linociera callophylla* (Blume) Knobl., but it proves to be remote from the species that Blume characterized. It belongs in the group with *Linociera pluriflora* Knobl., differing in its very rigid, thickly coriaceous leaves and shorter inflorescences. Other species in this assemblage are *L. nitens* Koord. and *L. verruculosa* Merr., but here again the vegetative characters alone separate this proposed new species.

Linociera stenura sp. nov.

Arbor glaberrima, ramulis ultimis gracilibus teretibus, 1 mm. diametro; foliis coriaceis, in sicco pallidis, vix vel obscure nitidis, utrinque subconcoloribus, lanceolatis vel oblongo-lanceolatis, basi acutis, 11–15 cm. longis, 2–4 cm. latis, ab infra medium sursum gradatim angustatis, apice longe graciliter caudato-acuminatis, acuminibus 1–2 cm. longis, obtusis; nervis primariis utrinque circiter 12, inter se plerumque 1–1.5 cm. distantibus, patulis, obscuris, 2–3 mm. a margine confluentibus, reticulis laxissimis, obscuris vel subobsoletis; petiolo 2.5 mm. longo; inflorescentiis axillaribus, solitariis, brevibus paucifloris, circiter 8 mm. longis, glabris; floribus usque ad 9, plerumque 3–5, breviter (1–1.5 mm.) pedicellatis, 4-meris, petalis linearibus, circiter 5 mm. longis, deorsum leviter ampliatis sed basi vix 0.5 mm. latis.

CELEBES: Malili District, *G. Kjellberg* 2120, August 19, 1929, a tree with white flowers on riverbank at Waraoe, altitude 50 m., TYPE in the Stockholm herbarium, a fragment in the herbarium of the Arnold Arboretum.

A species strikingly characterized by its distantly and obscurely nerved leaves which are very slenderly caudate-acuminate, gradually narrowed upward from below the middle, the obscure nerves spreading at nearly right angles and anastomosing with the equally inconspicuous and somewhat arched submarginal nerves 2–3 mm. from the leaf margin, the reticulations very lax, obscure or even subobsolete. Its few-flowered, axillary, solitary racemes are less than 1 cm. in length, even including the 5 mm. long very narrow petals.

Linociera ridleyi nom. nov.

Linociera cuspidate Ridl. Jour. Fed. Malay States Mus. 8 (4): 61. 1917, non Knobl. 1895.

The type of Ridley's species is a specimen collected on Korinchi Peak, Sumatra, at an altitude of about 7300 ft. He stated that it is allied to *Linociera montana* (Blume) DC. of Java.

Linociera sp.

Microtropis ? *lanceolata* Boerl. & Koord. in Koord.-Schum. Syst. Verzeich. Herb. Koord. 2: 33. 1911.

The type of this species is *Koorders 10283* from Sumatra, a fruiting specimen which in 1940, on the basis of an actual examination of the type in the Bogor herbarium, we could not place other than as a species of *Linociera*, perhaps allied to *L. oligantha* Merr.; see Merrill & Freeman, "The Old World species of the celastraceous genus *Microtropis* Wallich," Proc. Am. Acad. Arts Sci. 73: 307. 1940. It seems as unwise now to propose a new name for this imperfectly known species in *Linociera* as it did to us in 1940. However, to call attention to this misplaced entity, it has been considered desirable to make a record of it in the family and genus to which the species manifestly belongs. *Linociera lanceolata* Knobl. (1933), the name of a Santo Domingo species, invalidates the use of the epithet of Boerlage and Koorders in *Linociera*.

APOCYNACEAE

Microchites micrantha (Miq.) Hallier f. Jahrb. Hamb. Wissensch. Anstalt. 17: 156. 1899 (1900), *in nota*; Bakhuizen v. d. Brink in Backer, Beknopte Fl. Jav. 7B: Apoc. 32. 1948, *Blumea* 6: 389. 1950.

Otopetalum micranthum Miq. Fl. Ind. Bat. 2: 400. 1857, Versl. Meded. Kon. Akad. Wetensch. 6: 191. 1857.

Ecdysanthera schrieckii Van Huerck & Muell.-Arg. Obs. Bot. 191. 1870.

Microchites schrieckii Rolfe, Jour. Bot. 23: 214. 1885; Vidal, Phan. Cuming. Philipp. 126. 1885; Merr. Enum. Philipp. Fl. Pl. 3: 332. 1923.

Microchites polyantha sensu King & Gamble, Jour. As. Soc. Bengal 74 (2): 504. 1907 [Mater. Fl. Malay. Penin. 4 (no. 19): 714], non Miquel.

Trachelospermum philippinense Elm. Leaf. Philipp. Bot. 2: 488. 1908.

Microchites furcata Ridl. Jour. Roy. As. Soc. Straits Br. 79: 95. 1918, Fl. Malay Penin. 2: 368. 1923.

This adjustment in the nomenclature of *Microchites schrieckii* Rolfe, long considered to be a Philippine endemic, is necessary. Hallier f. in 1900, on the basis of a critical examination of its type specimen, determined the status of *Otopetalum micranthum* Miq. Miquel's description of its fruits as "Bacca corticata, semina intra pulpam fibrosum recepta (adhuc valde immatura)," and again in the species description as "baccae globosae ovoideae" is, of course, an impossible one for *Microchites*, the fruits of which are slender follicles; what he actually mistook for immature fruits were corolla tubes deformed by insects. Boerlage, Handl. Fl. Nederl. Ind. 2: 379-380. 1899, had discussed this case previous to Hallier's extensive consideration of it. The latter actually utilized nearly six pages of print

in his greatly detailed study of the problem, and even then succeeded in burying his new binomial in the text (p. 156) as "*Micrechites micrantha* m." where all bibliographers overlooked it for nearly half a century (it still is not listed in Index Kewensis); and at the same time its name-bringing synonym is equally buried in the text on page 152. I suspect that even Bakhuizen van den Brink might have overlooked this strangely published new binomial but for the fact that Hallier had added a reference on the type sheet to "Kautsch. Lianen p. 156. 1900"; this I noted, in the herbarium, and this it was that led me to Bakhuizen van den Brink's 1948 consideration of the case. I accept the synonymy as given by him, and add several other binomials.

The species, as I now understand it, extends from Siam and the Malay Peninsula (*Maingay 1081*) to Sumatra, Java, and also occurs more or less throughout the Philippines. There are, however, available for study only comparatively few collections except for the Philippine area, where about twenty are available. Among the previously unlisted ones are *McGregor* Bur. Sci. 47371 from Tayabas Province, Luzon, *Ebalo 940* from Basilan, and *Wenzel 3403* from Surigao Province, Mindanao. There are in the Leiden herbarium certain Javan collections named by Blume as representing *Tabernaemontana polyantha* Blume which actually represent *Micrechites micrantha* (Miq.) Hall. f., but there are also other specimens which represent *Micrechites polyantha* (Blume) Miq. as currently understood. I follow Bakhuizen van den Brink in his interpretation of *M. micrantha* (Miq.) Hall. f.

VERBENACEAE

Clerodendron fortunei Hemsl. Jour. Linn. Soc. Bot. 26: 259. 1890.

Clerodendron simile Merr. Govt. Lab. Publ. 35: 64. 1906, non Pearson (1901), *syn. nov.*

Clerodendron mindorensense Merr. Philipp. Jour. Sci. Bot. 7: 342. 1912. Enum. Philipp. Fl. Pl. 3: 404. 1923, *syn. nov.*

Hemsley's description of *Clerodendron fortunei* was based on two sheets of a *Fortune* collection merely indicated as coming from China. I had seen the type in 1935 and was then impressed with its close resemblance to certain Philippine forms. In September 1950 I again examined the type and compared it with specimens representing several Philippine species. I am now convinced that the *Fortune* specimens were taken from cultivated plants in China, for nothing like it has appeared in the very large collections made in southeastern and eastern China in the past thirty years. I do not hesitate to reduce the Philippine *C. simile* Merr. = *C. mindorensense* Merr. to *C. fortunei* Hemsl. Hemsley described the corollas as 2 in. long; the longest one I observed was 4 cm. in length. Those of *C. mindorensense* Merr. are 3 to 4 cm. long (original description 3 cm.). An allied form is *C. klemmei* Elm. from medium and higher altitudes in northern Luzon, but its corollas are 6 cm. in length.

Chinese associations with the Philippines have extended over a period

of about 2000 years. It is well known that they introduced into the Archipelago various economic plants, for a considerable number of these exotics are still known in the Philippines only by their Chinese names. Occasionally they also introduced an ornamental or merely curious species, as exemplified by Vidal's collection of the bignoniaceous *Markhamia caudafelina* (Hance) Craib in Albay Province, Luzon; see Sprague in Kew Bull. 1919: 310. 1919. The associations between Amoy and Manila were peculiarly close, and it may be that the Fortune collection came from plants cultivated at Amoy. On the other hand it is more than possible that they were taken from plants cultivated in the Fatee Gardens, across the river from Canton, which Fortune visited in 1843 and described the next year, Gard. Chron. 1844: 590. 1844. The Fatee Gardens still exist, being a series of nurseries on Lingnan Island where ornamental plants are propagated and sold. In the Philippines the species occurs at low altitudes, extending from northern Luzon to Mindoro, Semerara, Negros, and Mindanao. Additional collections at Kew are *Cuming* 1475 from Batangas Province, Luzon, *Vidal* 3453 from Laguna Province, Luzon, and *Loher* 4414 from central Luzon. There is a photograph of Hemsley's type in the herbarium of the Arnold Arboretum.

Clerodendron cyrtophyllum Turcz. Bull. Soc. Nat. Moscou 36(1): 222. 1863.

Clerodendron amplius Hance, Ann. Sci. Nat. Bot. V. 5: 233. 1866.

Clerodendron formosanum Maxim. Bull. Acad. Sci. St. Pétersb. 31: 85. 1886, Mém. Biolog. 12: 519. 1886.

Cordia venosa Hemsl. Jour. Linn. Soc. Bot. 26: 143. 1890.

My interest in looking up Hemsley's type in 1950 was inspired by the same motives as was the case with *Clerodendron fortunei* Hemsl.; that is, that in the Boraginaceae nothing appeared in the very large modern collections from Chekiang that have passed through my hands in the past thirty years that even suggested the species Hemsley characterized. The actual type of *Cordia venosa* Hemsl. is a fruiting specimen from Ningpo. A casual examination of the type in August 1950 indicated what the difficulty was, for it represents the very common *Clerodendron cyrtophyllum* Turcz., Hemsley having erred in placing his fruiting specimen in the boraginaceous genus *Cordia*; as the type specimen was mounted one would conclude from a casual examination that its leaves were alternate; on the contrary they are opposite. Rehder had added to the sheet "cf. *Clerodendron*," and later, Jour. Arnold Arb. 12: 76. 1931, had actually reduced Hemsley's species to *Clerodendron cyrtophyllum* Turcz. This very common and characteristic species is now represented in the herbarium of the Arnold Arboretum by approximately a hundred individual collections, twenty-five of which are from Chekiang. Other areas represented are Anhwei, Hunan, Kiangsu, Kwangsi, Kweichow, Fukien, and Kwangtung provinces, Formosa, Hainan, and Indo-China. There is a photograph of Hemsley's type in the herbarium of the Arnold Arboretum.

RUBIACEAE

***Canthium tavoyanum* (Parker) comb. nov.**

Plectronia tavoyana Parker, Kew Bull. 1925: 429. 1925. Burma.

This change is made for the obvious reason that the generic name *Plectronia* Linnaeus has been misapplied by many modern botanists. The Linnaean type is a representative of the oliniaceous genus *Olinia* Thunberg. See Merrill, Philipp. Jour. Sci. 35: 7. 1928.

***Dentella serpyllifolia* Wall. ms. "in sched. in Herb. Wall. sub 6206G."**
1832, *nom. nud.*; Craib, Fl. Siam Enum. 2: 27. 1932, *nom. subnud.*;
Airy-Shaw, Kew Bull. 1932: 289. 1932, *descr.*

LUZON: Rizal Province, *Bur. Sci.* 1398, August 1906, distributed as *Dentella repens* J. R. & G. Forster.

Curiously Wallich's accepted name does not appear in his lithographed List (generally cited as Catalogue), but Airy-Shaw apparently found it on a subsidiary label in the master set at Kew. The entry in the distributed lithographed List is under *Dentella repens* Forst., 6206"G? Ripa Irawaddi ad Henzada — 1826. (F[1]os distincta)." The species is now known to extend from Assam and northern Bengal to Burma, Siam, Lombok, Java, Mauritius, Luzon, and Guam (*Fosberg*). Curiously *Dentella repens* J. R. & G. Forst. has also been found in Guam, an intermediary stop, and at Acapulco, the terminus of the Manila-Acapulco galleon line (1565–1815). Both species are ruderals probably in part distributed by migratory birds, partly by man. This species is otherwise recorded from Polynesia only from the Marquesas Islands.

***Ophiorrhiza sarawakensis* nom. nov.**

Ophiorrhiza reticulata Ridl. Sarawak Mus. Jour. 1 (2): 32. 1912, non Korth. (1851).

A new name is needed for the Bornean species characterized by Ridley in 1912.

***Psychotria polytricha* Miq. Fl. Ind. Bat. 2: 287. 1857.**

Psychotria rufipila Val. Ic. Bogor. 3: 253, *pl.* 291. 1909, *syn. nov.*

Psychotria trichophlebia Merr. Mitt. Inst. Bot. Hamburg 7: 295. 1937, *syn. nov.*

I now think but a single species is represented here. Miquel's species was based on *Korthals* specimens from Sumatra and Borneo; that of Valeton on Bornean specimens, *Teysmann* 8000 and *Jaheri* 509; and that of myself on *Winkler* 1571, from Borneo. I have seen none of the cited specimens representing Valeton's species, but my concept of its limits is gained from his excellent illustration and ample description. *Beccari* 822, from Sumatra, in fruit, is currently referred to this species. There are

several old sheets at Leiden where the original records were lost or confused, labeled "Sumatra," "Moluccas" (this scratched), and "Java" (this very doubtful). I suspect that these were all from Sumatra or Borneo.

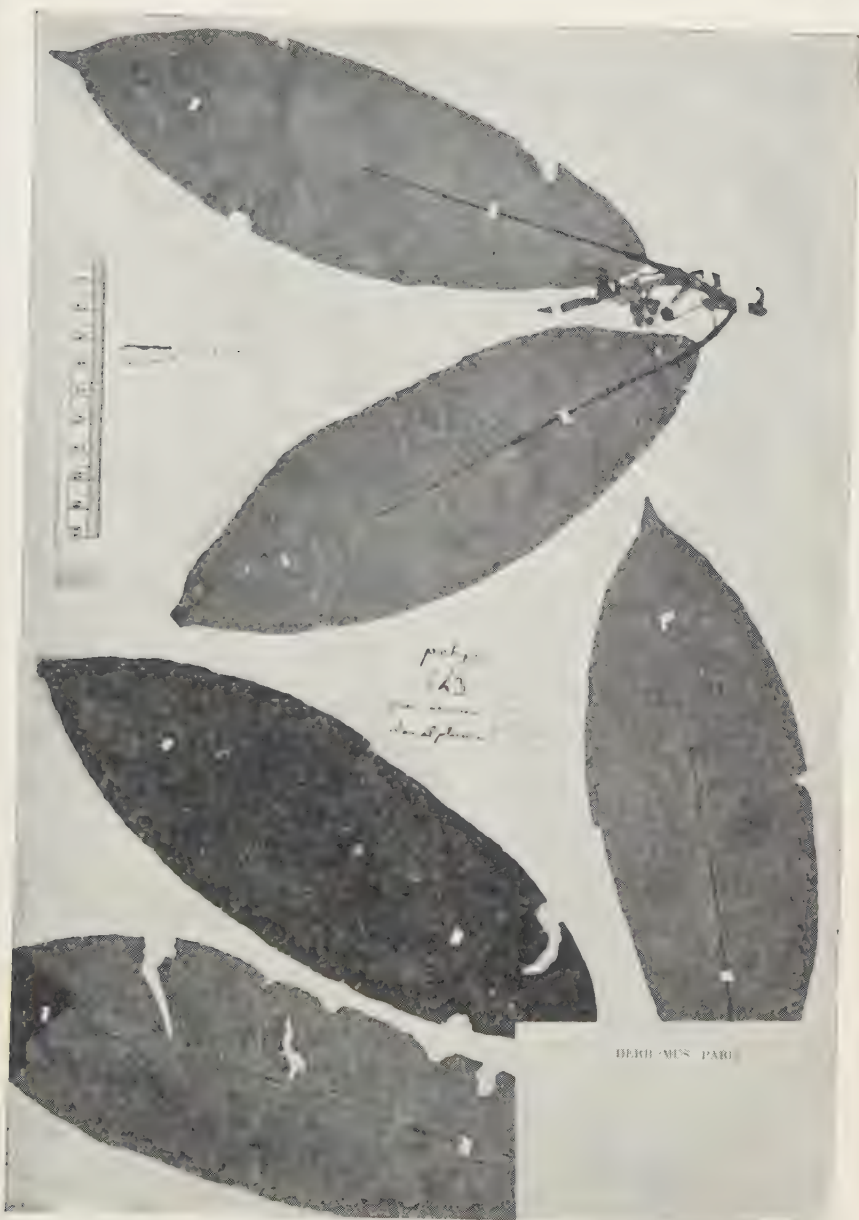
***Psychotria sangeana* (Miq.) comb. nov.**

Chasalia sangeana Miq. Fl. Ind. Bat. Suppl. 546. 1862.

Psychotria rhodocarpa Teijsm. & Binn. Nat. Tijdschr. Nederl. Ind. 27: 30. 1864.

The type of Miquel's species was a *Teysmann* specimen from Sumatra. On the basis of the material in the Rijksherbarium representing two supposedly distinct species in different genera, both sent by Teysmann, I see no tangible differences and, although fruits are absent, I believe *Psychotria* to be its proper generic designation. Apparently at one time Valetton thought that *Uragoga* was represented, and later that the plant might be a small form of *Psychotria expansa* Blume. Miquel's older name is here adopted.

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SAURAUIA LANCEOLATA DC.
(TYPE, *Leschenault 643*)

STUDIES IN THE BORAGINACEAE, XXVII
SOME GENERAL OBSERVATIONS CONCERNING
THE LITHOSPERMEAE

IVAN M. JOHNSTON

IN THE PREVIOUS PAPERS of this series the genera composing the tribe Lithospermeae have been redescribed and individually discussed, Jour. Arnold Arb. 34: 258-299 (1953) and 35: 1-81 (1954). The tribe having been surveyed, we are now prepared to present a new key to the twenty-three genera concerned, and also some general observations concerning the tribe as a whole. Listed alphabetically the twenty-three genera of the Lithospermeae are as follows: *Alkanna*, *Ancistrocarya*, *Arnebia*, *Buglossoides*, *Cerithe*, *Cystistemon* (includes *Vaupelia*), *Echioides*, *Echium*, *Halacsya*, **Lasiarrhenum*, *Lithodora*, *Lithospermum*, *Lobostemon*, **Macromeria*, *Maharanga*, *Moltkia*, **Nomosa*, *Onosma*, **Onosmodium*, **Peritostema*, *Podonosma*, **Psilolaemus*, and *Stenosolenium*. Six of the twenty-three genera are endemic to America (those marked with the asterisk), and sixteen are endemic to the Old World. Only one genus, *Lithospermum*, has species present in both the Old and the New World.

To be excluded from the Lithospermeae are a number of genera which at one time or another have been referred to it. These include *Moritzia*, *Thaumatocaryon*, *Antiphytum*, *Amblynotopsis*, *Amphibologyne*, *Sericostoma*, *Echiochilon*, *Megastoma*, *Myosotis*, *Mertensia*, *Trigonotis*, *Pulmonaria*, *Bothriospermum*, *Moltkiopsis*, *Mairetis* and *Neatostema*. Of these genera, *Pulmonaria* is best referred to the Anchuseae and *Bothriospermum* to the Cynoglosseae, and the remaining fourteen to the Eritricheae.

As to habit the Lithospermeae are prevailingly herbaceous perennials. Species having only an annual duration are relatively few and occur only in *Buglossoides*, *Arnebia*, *Stenosolenium*, *Cystistemon* (including *Vaupelia*), *Echium*, and *Cerithe*. The cymes are abundantly bracted and usually conspicuously so in all members of the tribe except *Ancistrocarya*. Floral dimorphy in several forms is present in five genera within the tribe. Heterostyly in a very elaborate form is present in *Lithospermum*, *Echioides*, and *Arnebia*, and in a simple form in *Lithodora*. Elsewhere among the Boraginoideae heterostyly is reported only among species of *Anchusa* and *Pulmonaria* of the Anchuseae, among *Mertensia*, *Cryptantha*, and *Amsinckia* in the Eritricheae, and in one species of *Paracaryum* in the Cynoglosseae. Gynodioecism is widespread within *Echium*. Outside the Lithospermeae it is known only in a few species of *Myosotis* and *Lindelofia*. Cleistogamy is developed in some species of *Lithospermum* and elsewhere in the subfamily is known only in *Neatostema*, *Cryptantha* and *Pectocarya*.

Deviations from radial symmetry in the flower are more common and widespread in the Lithospermeae than in any other group within the family. The corolla becomes distinctly zygomorphic in *Echium*, *Lobostemon*, *Halacsya*, *Alkanna*, and *Macromeria*. In addition, zygomorphy less evidently developed is also present in corollas of some species of *Cerithe* and *Onosma*. Deviations from radial symmetry in the androecium occur in many Lithospermeae. Within the corolla the individual filaments may differ from one another in length, or in the form of their attachment, or in the height at which they are affixed to the corolla. Androecia deviating from radial symmetry occur in *Echium*, *Lobostemon*, *Alkanna*, *Moltkia*, *Lithodora*, *Maharanga*, *Cerithe*, *Echioides*, *Arnebia*, *Stenosolenium*, and *Macromeria*. Outside the Lithospermeae decidedly zygomorphic corollas occur only in *Echiochilon* and *Lycopsis*. Differentiation among the members of the androecium, within the corolla, occur outside the Lithospermeae in *Echiochilon*, *Moltkiopsis*, *Lycopsis*, *Caccinia* (includes *Heliocarya*) and *Amsinckia*.

The frequency of yellow or orange as a corolla-color among the Lithospermeae is also noteworthy. Orange, yellow, or decidedly yellowish corollas occur in *Moltkia*, *Halacsya*, *Alkanna*, *Onosma*, *Podonosma*, *Cerithe*, *Lithospermum*, *Echioides*, *Arnebia*, *Psilolaemus*, *Perittostema*, *Onosmodium*, and *Macromeria*. Within the tribe blue or bluish or pink corollas occur in *Echium*, *Lobostemon*, *Alkanna*, *Moltkia*, *Lithodora*, *Maharanga*, *Onosma*, *Cystistemon*, *Podonosma*, *Cerithe*, *Arnebia*, *Stenosolenium*, *Buglossoides*, and *Ancistrocarya*. White corollas are normal in species of *Lithospermum*, *Buglossoides*, *Lasiarrhenum*, *Nomosa*, and *Onosmodium*. Blue, pinkish, or white corollas predominate in the other tribes of the Boraginoideae. Orange, yellow or yellowish corollas, however, are developed in other tribes by only a relatively few species of *Nonnea*, *Symphytum*, *Anchusa*, *Neatostema*, *Cryptantha*, *Hackelia*, *Amsinckia*, *Rindera*, *Lindelofia*, and *Cynoglossum*.

The corolla has an unappendaged throat in seventeen of the twenty-three genera of the Lithospermeae. Within the tribe there are only six genera in which intrusive faucal appendages are developed, viz. *Lithospermum*, *Buglossoides*, *Macromeria*, *Perittostema*, *Halacsya* and *Alkanna*. In the three other tribes of the Boraginoideae, however, the corolla is almost always provided with faucal appendages. Indeed, within the Anchuseae, Eritrichieae and Cynoglosseae there are only eight genera, out of more than sixty, in which the corolla is devoid of faucal appendages in all or nearly all of the species, i.e., *Moltkiopsis*, *Mairetis*, *Neatostema*, *Echiochilon*, *Sericostoma*, *Amphibologyne*, *Amsinckia* and *Trichodesma*. In the other genera in these three tribes the faucal appendages are well developed or are weak or absent only in a few species in which the corolla is much reduced in size, e.g., *Cryptantha*, *Plagiobothrys*, and *Pectocarya*.

The corollas of the Lithospermeae, unlike those in other tribes of the family, may bear stipitate glands on their inner surfaces, particularly so those in and directly below the corolla-throat. Stiped glands, sometimes in considerable abundance, are a feature inside the corollas of some or all

species of *Lithospermum*, *Macromeria*, *Lasiarrhenum*, *Perittostema*, *Arnebia*, *Buglossoides*, *Lithodora*, and *Alkanna*.

The corolla-throat in *Ancistrocarya* and in one species of *Lithodora* is densely strigose, a condition paralleled outside the tribes only in *Sericostoma* and *Echiochilon*. The corolla-tube (as distinguished from the corolla-throat) is hairy in species of *Lithospermum*, *Macromeria*, *Echioides*, and *Arnebia*. Outside of the Lithospermeae I know of a comparable condition only in the flowers of species of *Neatostema*, *Mertensia*, *Amsinckia*, and *Rochelia*.

The stamens in the Lithospermeae show a number of unusual features. In *Cerinthe*, *Podonosma*, *Cystistemon*, *Onosma*, and *Maharanga*, the anthers are connivent and become joined, in *Cerinthe* by the entangling of the caudate bases of the thecae, and in the other genera by lateral cohesion of the anthers. Outside of the Lithospermeae this condition is most closely approximated in *Borago* and *Trichodesma*. In these two genera the anthers are connivent, but in *Borago* they remain distinct, while in *Trichodesma* they become joined by the entangling of their contorted tips.

The anthers are terminated by an elongate sterile appendage in *Cerinthe*, *Podonosma*, *Onosma*, *Cystistemon*, *Maharanga*, and *Nomosa*. Outside of the present tribe only in *Trichodesma* of the Cynoglosseae does a comparable very elongate appendage terminate the anther. Small appendages terminate the anther in *Halacsya*, *Onosmodium*, *Lasiarrhenum*, and *Buglossoides*. Outside the tribe I know of such moderately appendaged anthers only in *Myosotis* and *Rochelia*.

In *Lasiarrhenum*, *Nomosa*, and one species of *Macromeria* the connective on the dorsum of the anther is hairy, and in *Halacsya* the margins of the thecae are densely short-ciliate. These conditions appear to be unique in the family.

The filaments within the individual corolla are not whorled but affixed at different elevations above the corolla-base in species of *Lithodora*, *Alkanna*, *Echium*, *Lobostemon*, *Macromeria*, *Stenosolenium*, *Arnebia*, and *Echioides*. This unusual behavior is duplicated outside of the Lithospermeae only in *Echiochilon*, *Lycopsis*, and *Amsinckia*. The five filaments within the corolla are of different lengths in species of *Arnebia*, *Moltkia*, *Alkanna*, *Echium*, and *Lobostemon*. Outside of this tribe I know of this latter condition only in *Moltkiopsis*, *Echiochilon*, and *Caccinia*.

Although the pollen of the Boraginaceae, outside of the Lithospermeae, has not been systematically studied, there have been enough random examinations to indicate that the pollen of the Lithospermeae is notable for a high frequency of asymmetric types. Such pollen has the upper and lower halves of the grain differing in size and configuration. In lateral outline the grain may be ovate, conic-ovate, oblong-ovate, or be constricted above the pores and approach the outline of an hour-glass or a shoe-print. It is encircled by a row of pores, not about the equator, but below it, where the grain has its maximum diameter. Pollen of this sort is developed in *Alkanna*, *Echium*, *Lobostemon*, *Macromeria*, *Onosmodium*, *Nomosa*, *Lasiarrhenum*, *Ancistrocarya*, *Lithospermum*, *Podonosma*, *Cysti-*

stemon, and *Onosma*. At present this type of pollen is known only in genera of the Lithospermeae.

The style in the Lithospermeae may be short to elongate and be either included in the corolla or exerted from it. In *Arnebia* it may be simple, bilobed, forked, or bis-bifid. It is simply forked in *Echium* and *Stenosolenium* and frequently bilobed in *Lithodora* and *Alkanna*. The forked or bilobed style is not duplicated in other tribes of the Boraginoideae. Each lobe of the forked style is usually terminated by a stigma. When the style is simple it commonly bears two stigmas juxtaposed and terminal on its summit. In some genera, however, the two stigmas are separated and frequently over-topped by a bilobed sterile apex of the stylar column. In such cases the stigmas assume a subterminal position on the style and may become evidently lateral on it.

The subterminal stigmas are best developed in species of *Buglossoides* and *Lithospermum*. Unless the peculiar stigma of *Myosotis* proves to be similar, subterminal stigmas are well developed in other tribes of the Boraginoideae only in the genus *Sericostoma*. In most genera of the Lithospermeae the style is terminated by a pair of juxtaposed stigmas. Within the tribe the two stigmas usually remain distinct. In other tribes of the subfamily they are prevailingly united.

The nutlets of the Lithospermeae are prevailingly straight, erect, and basifixed, and in form are either ellipsoidal (and usually plump) or they are ovoid with the venter tending to be angulate and the apex coarsely beaked. Nutlets that are strongly compressed dorsi-ventrally, though frequent in the Eritrichieae and Cynoglosseae, are rare in the Lithospermeae and indeed are practically restricted to a few species of *Arnebia*. The ventral keel in various degrees may be obscure, broad and rounded, or narrow and prominent. There may be no evidence of a ventral suture or the suture may be marked only by a line that may be indistinct or sometimes interrupted. The suture is always tightly closed with its margins usually fused or firmly joined and never overlapping.

Several genera of the tribe have nutlets sufficiently unusual to be deserving of special comment. The 2-celled, 2-seeded nutlets of *Cerinth* are well known. They apparently represent the congenital union of a pair of single-seeded nutlets. The condition is unique in the Boraginoideae. Also unique is the form of the nutlets of *Ancistrocarya*. From just above the broad base these gradually narrow into a very prolonged, slender, curved, sword-like beak which is hamate at the apex. The beak, which is nearly as long as the fertile portion of the nutlet, is a sterile prolongation of the pericarp-apex.

The bent nutlets of *Moltkia*, *Halacsya*, *Alkanna*, *Podonosma*, and some insular species of *Echium* represent another very unusual form of nutlet. Outside the tribe it is weakly represented only in *Neatostema* and some species of *Plagiobothrys*. In the Lithospermeae mentioned, the nutlets are basally affixed to the gynobase but only the lower half of the nutlet is erect. Above their middle they are bent 30–130° towards the ventral side. The seed within the nutlet is also bent. The cotyledons are vertical to

the attachment-end of the nutlet and the tip of the cotyledons is directly above the nutlet-attachment, the proper relation in a basifixed nutlet. In *Alkanna* and *Podonosma* the nutlet-body is so strongly curved that the attachment actually has the appearance of being lateral.

The nutlets of the Boraginoideae characteristically have a more or less convex dorsum and a usually angulate or medially carinate venter. An extreme departure from this conventional form is found in the nutlets of *Arnebia tetrastigma*. In that species, the sole member of *Arnebia* § *Euarnebia*, the nutlet has a plane or even slightly concave dorsum and a venter that is broadly convex with the ventral keel only very obscurely developed. The nutlets are also aberrant in having a cordate base and a T-shaped scar.

The nutlet of *Stenosolenium* bears its attachment-scar not sessile on the base of the nutlet-body but rather ventral to the proper base of the nutlet at the lower end of a downwardly directed hollow stipe originating high up on the ventral side of the nutlet. In all other genera of the Lithospermeae the attachment is on the base of the nutlet-body. It is small, short and substipitate in *Alkanna* and *Podonosma* but is relatively large, sessile, and commonly flabellate or ovate in other genera. The attachment is usually restricted to the base of the nutlet. In *Arnebia guttata* and *A. tetrastigma*, however, it has a noticeable prolongation upwards for a short distance above the base on the nutlet-venter. As a consequence it becomes somewhat T-shaped, especially in *A. tetrastigma*.

The attachment-scar is usually not only basal on the nutlet but also horizontal. When oblique it usually slopes upward only towards the ventral side of the nutlet-body and commonly only slightly so. A basal attachment-scar sloping upward, not towards the venter of the nutlet but rather towards the dorsum, is present only in *Buglossoides* § *Eubuglossoides* and perhaps in *Ancistrocarya*. The attachment of the nutlets in *Lithodora* is anomalous. The true base of the nutlet is permanently affixed to the gynobase, the nutlet being freed along a new plane of abscission developed a short distance above the morphological base of the nutlet.

The nutlets of the Lithospermeae may be smooth, verrucose, tumulose, or rugose, and the epidermis lustrous or opaque and smooth and shiny or minutely muriculate, verruculose, or papillate. The smooth, lustrous, pallid, porcelain-like nutlets characteristic of most species of *Lithospermum* occur elsewhere in the tribe only in *Macromeria*, *Onosmodium*, *Lasianrhenum*, *Psilolaemus*, *Ancistrocarya*, and *Buglossoides* § *Margarospermum*. Roughened or at least opaque nutlets prevail in other genera of this group. In other tribes of the Boraginoideae the nutlets may be armed with numerous glochidiate subulate appendages, or the back of the nutlet may bear a coroniform or annulate appendage, or it may be encircled by an entire, toothed or lobed, spreading or upturned margin. Among the genera of the Lithospermeae, however, only a few species, in *Onosma*, *Echium*, and *Ancistrocarya*, have appendaged nutlets. Those of *Onosma tricerospermum* Lag., of Spain, bear three conspicuous spreading rigid subulate spines on the dorsum. The nutlets of all other species of *Onosma*

are unappendaged. In some of the Canary Island species of *Echium* (cf. Webb. & Berth., Phytogr. Canar. t. 146, 1844), the pericarp develops a few very exaggerated protuberances that give the nutlet the appearance of being coarsely lobed. The slenderly rostrate nutlets of *Ancistrocarya* have already been described. The nutlets of the Lithospermeae (like those of the Anchuseae) never bear glochidiate appendages nor epidorsal annulate or coroniform crests, nor is the back ever encircled by a differentiated margin.

My observations as to the orientation of the zygomorphic corollas in the Boraginoideae do not accord with the much quoted classical statements of the matter by Döll, Fl. Baden 2: 775-6, 778 (1859) and Eichler, Blüthendiagramme 1: 197 (1875). The calyx lobes of the boraginaceous flower are numbered by Eichler in the following order, 1, 3, 5, 2, and 4. Lobe no. 2 is identified as the one at the rear of the flower and as having a position opposite the rachis of the scorpioid cyme. This order appears to be correct, for in those flowers having very unequal calyx-lobes (e.g., *Cerithe*) the largest outermost lobe, i.e., no. 1 according to Eichler, is always one of the two lobes on the abaxial or front side of the flower. With the calyx-lobes recognized as serviceable points of reference, it can be stated that according to Eichler the axis of the irregular corolla of *Echium* passes between the corolla-lobes alternating with calyx-lobe no. 4 and through the middle of the corolla-lobe alternating with calyx-lobes nos. 3 and 5. This gives the flowers of *Echium* a very strongly oblique plane of symmetry and places the 2-lobed lip of the corolla on the adaxial side of the flower.

In my study of herbarium material, I have found in *Echium*, *Lobostemon*, *Halacsya*, *Alkanna*, *Lycopsis*, and *Amsinckia*, that the axis in the bilaterally symmetrical corolla is oriented in such a manner that the 2-lobed lip of the corolla is abaxial and the 3-lobed lip adaxial. In these genera the plane of symmetry is only weakly oblique. It passes through the middle of the rear corolla-lobe (that alternating with calyx-lobes nos. 4 and 2) and between the corolla-lobes alternating with calyx-lobe no. 3. This is the same orientation that prevails in the zygomorphic corollas of the Solanaceae. It represents a deviation of only 36° from a truly medial orientation, not 72° as called for by Eichler.

Only in *Macromeria*, *Echiochilon*, and *Heliocarya* have I found in the Boraginaceae zygomorphic corollas with medial orientation, that is to say, so oriented that the rear (adaxial) lip was 2-lobed and the abaxial lip 3-lobed. In the flowers of these genera the axis apparently passes between the two rear corolla-lobes (those alternating with calyx-lobe no. 2) and also through the middle of the forward corolla-lobe, that alternating with calyx-lobes nos. 1 and 3. Medial orientation similar to this prevails in the corollas of the Verbenaceae and Labiatae. It represents an angular deviation of 36° from the axis of symmetry in *Echium*.

Enough evidence has accumulated from the study of herbarium specimens to cast considerable doubt on the accuracy of accounts in the books concerning the orientation of the bilaterally symmetric flowers of the Bora-

ginoideae. What is now needed is observations of flowers in the fresh state. The orientation should be determined not merely in the flowers having evidently zygomorphic corollas, but also in those in which the corolla may be only very obscurely bilateral or which depart from radial symmetry only in the androecium. Studies of symmetry are especially needed in *Lithodora*, *Moltkia*, *Stenosolenium*, *Arnebia*, *Echioides*, *Cerinthe*, *Onosma*, *Podonosma*, and *Moltkiopsis*. The orientation in the corolla of these genera needs to be determined not only in relation to the axis of the cyme, but also in relation to calyx-lobe no. 1, and particularly so when the latter is distinguishable by its size.

KEY TO THE GENERA OF THE LITHOSPERMEAE

Pollen bearing only 3 pores, grains in polar profile usually distinctly 3-sided.

Pollen-grains evidently colpate; thecae not ciliate; flowers not precociously sexual.

Nutlets strongly incurved, near the middle bent 90–130°, the attachment small and substipitate, appearing to be lateral but actually basal on the short erect lower section of the nutlet; herbage usually glanduliferous.

Corolla-lobes narrowly triangular, acute, soon reflexed; corolla-throat glabrous and devoid of faucal appendages and stipitate glands; anthers partially exserted. **Podonosma.**

Corolla-lobes rounded, spreading; corolla-throat usually bearing stipitate glands; stamens and faucal appendages borne low in the corolla-throat and hence deeply included. **Alkanna.**

Nutlets straight (or rarely bent in *Echium*); herbage not glanduliferous.

Anther lacking a prolonged sterile tip, remaining distinct; corolla usually evidently zygomorphic.

Annulus borne 1 mm. or less above the base of corolla-tube, composed of a minute collar or a ring of 5–10 minute sparingly hairy lobules; style almost always 2-lobed. **Echium.**

Annulus developed 1.5–6 mm. above the corolla-base, represented by 5 evident densely villous swellings or 5 squamose appendages borne below the attachment of each stamen; style simple. **Lobostemon.**

Anther narrowed into a prolonged terminal appendage, commonly adnate at the base or along the sides to form a synandrium; corolla regular or practically so.

Corolla-lobes well developed, as long as or much longer than the corolla-tube, spreading or decurved; anthers coherent only along the margins of the terminal appendage, appendage evidently longer than the theca; filaments very short and usually bearing a thickened hairy basal appendage; tropical Arabia and Africa. **Cystistemon and Vaupelia.**

Corolla-lobes short, commonly about as long as broad, conspicuously much shorter than the tubular portion of the corolla; anthers usually coherent at the base and frequently also along the margin of the thecae and even along the margin of the terminal appendage, appendage usually shorter than the theca; filaments usually elongate, not appendaged at the base.

Calyx-lobes narrow, elongate, more or less parallel, separated by a

- very narrow usually closed sinus; corolla without ribs projecting outward between the calyx-lobes; pollen ovoid to sphaeric or strongly oblate **Onosma.**
- Calyx-lobes more or less triangular, separated by an open triangular sinus; corolla with puffed-out ribs that project outward between the calyx-lobes; pollen cylindric or vertically ellipsoid. Himalaya and southwestern China **Maharanga.**
- Pollen-grains not at all colpate; anthers with thecae margined by a ciliate fringe of short stout crowded hairs; flowers precociously sexual, style and stamens exserted while the corolla is still incompletely developed; nutlets bent **Halacsya.**
- Pollen bearing 6 to many pores; grains circular or somewhat polygonal in polar profile.
- Nutlets united in pairs, each nutlet 2-locular and 2-seeded; pollen evidently colpate; leaves cordate-amplexicaul at base **Cerinth.**
- Nutlets not united, each one 1-celled and 1-seeded; pollen obscurely if at all colpate; leaves not cordate-amplexicaul.
- Pollen-grains bearing 2 rows of pores, one at each end of the elongate grain.
- Nutlet-attachment at the base of a downwardly directed stipe originating on the ventral side of the ascending nutlet-body ... **Stenosolenium.**
- Nutlet-attachment on the base of the nutlet-body **Arnebia.**
- Pollen bearing only a single encircling row of pores.
- Nutlets circumscissile above the base, their major seminiferous portion falling away leaving the short basal section persisting as a usually cupulate appendage permanently affixed to the gynobase .. **Lithodora.**
- Nutlets detaching at the very base.
- Throat of corolla glabrous and also devoid of stiped glands and faucal appendages.
- Nutlets evidently bent at or near the middle; corolla blue or purple, or (in one species) yellow; filament evidently exserted from corolla-throat except in one species **Moltkia.**
- Nutlets straight.
- Corolla salverform, the broad spreading yellow limb usually decorated with 5 evanescent black or purplish spots; stamens borne at unequal heights in the corolla-tube; Armenia, Caucasus and Azerbaijan **Echioides.**
- Corolla tubular, white or yellow, bearing no dark evanescent spots, lobes erect or ascending; stamens all arising at the same height in the corolla-throat; American.
- Filaments about half the total length of the corolla, arising well below the middle of the corolla, base of filaments shaggy with slender multicellular gland-tipped hairs **Nomosa.**
- Filaments about one tenth the length of the corolla or less, arising above the middle of the corolla, glabrous throughout.
- Corolla-lobes narrow, acute or acuminate, very narrowly imbricate in the bud, sinus between lobes plicate, inflexed and thickened at base; pollen ovoid; leaves coarsely veined **Onosmodium.**
- Corolla-lobes ovate, broadly imbricate in the bud, sinus between lobes not plicate nor inflexed nor thickened at base; pollen ellipsoidal; leaves veinless or nearly so **Psilolaemus.**

Throat of corolla decorated with appendages, stipitate glands or abundant hairs.

Nutlets gradually narrowed into a very prolonged beak, conspicuously rostrate with the tip hamate; cymes bractless above the very base; corolla-throat abundantly villose-strigose . . . **Ancistrocarya.**

Nutlets not conspicuously rostrate, not hamate at the apex; cymes bracted throughout; corolla-throat not conspicuously hairy.

Filaments broadening upwards from the attachment, above the middle evidently broader than at the base.

Anthers conspicuously hairy on the back; filaments oblanceolate; corolla lacking faucal appendages; leaves broad and conspicuously veined **Lasiarrhenum.**

Anthers glabrous, filaments deltoid to obovoid; corolla with faucal appendages; leaves very narrow, veinless **Perittostema.**

Filaments linear or subulate or unguiculate.

Anthers completely exerted from the corolla-throat; corolla large, 39–90 mm. long, trumpet-shaped; filaments 6–70 mm. long **Macromeria.**

Anthers completely included or only partially exerted from the corolla-throat; corolla usually less than 40 mm. long, salverform, funnelform or subtubular; filaments 0.5–5 mm. long.

Corolla-throat decorated inside with 5 well-developed vertical lines of hairs and stiped-glands **Buglossoides.**

Corolla-throat lacking very well developed vertical lines of hairs and stiped glands, bearing localized faucal appendages or bearing scattered or localized congregations of stiped glands **Lithospermum.**

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ECOTYPIC VARIATION OF THE PHOTOPERIODIC
RESPONSE IN *POPULUS*SCOTT S. PAULEY¹ AND THOMAS O. PERRY²*With eight text-figures*

INTRODUCTION

DURING THE PAST FEW DECADES, the traditional and complacent notion that genetic differences within tree species are nonexistent or negligible has been gradually discarded. Most silviculturists are no longer content with the assumption that diversity within tree species can be adequately explained in terms of environment alone. Such a fundamental revision in biological theory has, quite naturally, produced a marked impact on silvical research methods and silvicultural practice.

The limitations, for example, of the descriptive method as a means of analyzing intraspecific diversity have become increasingly apparent. Although field observation and description of phenotypes and environment provide useful and essential preliminary data for the analysis of observed diversity, the method provides no means for determining the relative amounts of environmental fluctuation and genetic variation involved.

The solution of such silvical problems is, however, possible by transplant methods that have been perfected by various workers (Turesson, 19; Turrill, 20; Clausen, Keck and Heisey, 2; and others). One application involves the transplantation of different genetic types into a uniform environment. Under such conditions the effects of differences in habitat on the phenotype are eliminated, and the genotypes of different individuals of the group under investigation may be compared directly. For information on the rigidity or plasticity of genotypes, wild representatives of the species may be propagated vegetatively, and the clonal lines thus established may be planted under different environmental conditions. Both methods have been used in the photoperiodic studies here reported, and form one of the approaches to silvical problems currently under investigation by the Cabot Foundation.

Source of Material

Initial sampling of wild populations in *Populus* species native to North America was begun in the fall and winter of 1947-48, and has been continued annually since that time. During the period 1947-50 principal emphasis was placed on obtaining representatives of *P. trichocarpa* (western balsam poplar or so-called "northern black cottonwood"), native of the

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Pacific coast region, and the *P. deltoides* complex (eastern cottonwood) of the eastern United States. These collections were all in the form of branch or stem cuttings taken from what were determined to be average, healthy specimens growing under natural conditions at the various collection points. The use of cuttings was designed to insure that the clonal lines represented were derived from individuals known to be capable of survival in their native habitat. Since species in the section *TACAMAHACA* (balsam poplars) are uniformly good rooters from plants of any age, there was no need to restrict selected individuals of *P. trichocarpa* to the younger age classes. On the other hand, because of the poor rootability of cuttings from old trees, almost all of the *P. deltoides* clonal lines established were started from cuttings taken from plants 2 to 6 years of age.

The photoperiodic studies here reported are primarily concerned with clones of *P. trichocarpa* and the *P. deltoides* complex collected during the period 1947-50; but reference is also made to clonal line collections of *P. tacamahaca* (balsam poplar) made during the same period, and to collections of various other *Populus* species acquired in the spring of 1950 and subsequently.

Approximate ranges of *P. trichocarpa* and *P. deltoides* and the locality of origin for the various clonal lines of these species used in the photoperiodic studies are shown in FIGURE 1.

Although a portion of the field collection was done by the senior author, the bulk of the material was made available through the generous assistance and cooperation provided by numerous state and federal forestry agencies in the United States, and similar provincial and dominion organizations in Canada. Especially extensive contributions have been made by the U. S. Forest Service, U. S. Soil Conservation Service, Dominion Forest Service, and many state and provincial conservation departments within the ranges of the species concerned.

Experimental Areas

The principal propagation and test plantation site utilized by the Cabot Foundation is located in the town of Weston, Middlesex County, Massachusetts, about 10 miles west of Boston. The area is part of the former Case Estate, given to the Arnold Arboretum about a decade ago. The portion of several acres which has been allocated to the Cabot Foundation was formerly used as a pasture or mowing. The soil is, in general, uniform and the surface flat. The elevation is 200 feet, and lies somewhat lower than most of the surrounding area. For this reason temperature inversions in early fall may result in a somewhat shorter frost-free season than the average of 148 days for the Weston area as based on records of the Weston Weather Bureau Station (located ca. 2 miles northwest of the Case Estate at an elevation of 224 feet).

A portion of the Weston tract has been devoted to the propagation of the clonal lines assembled since the 1947-48 season, while the remainder of the area has been set aside for the establishment of permanent test plantations.

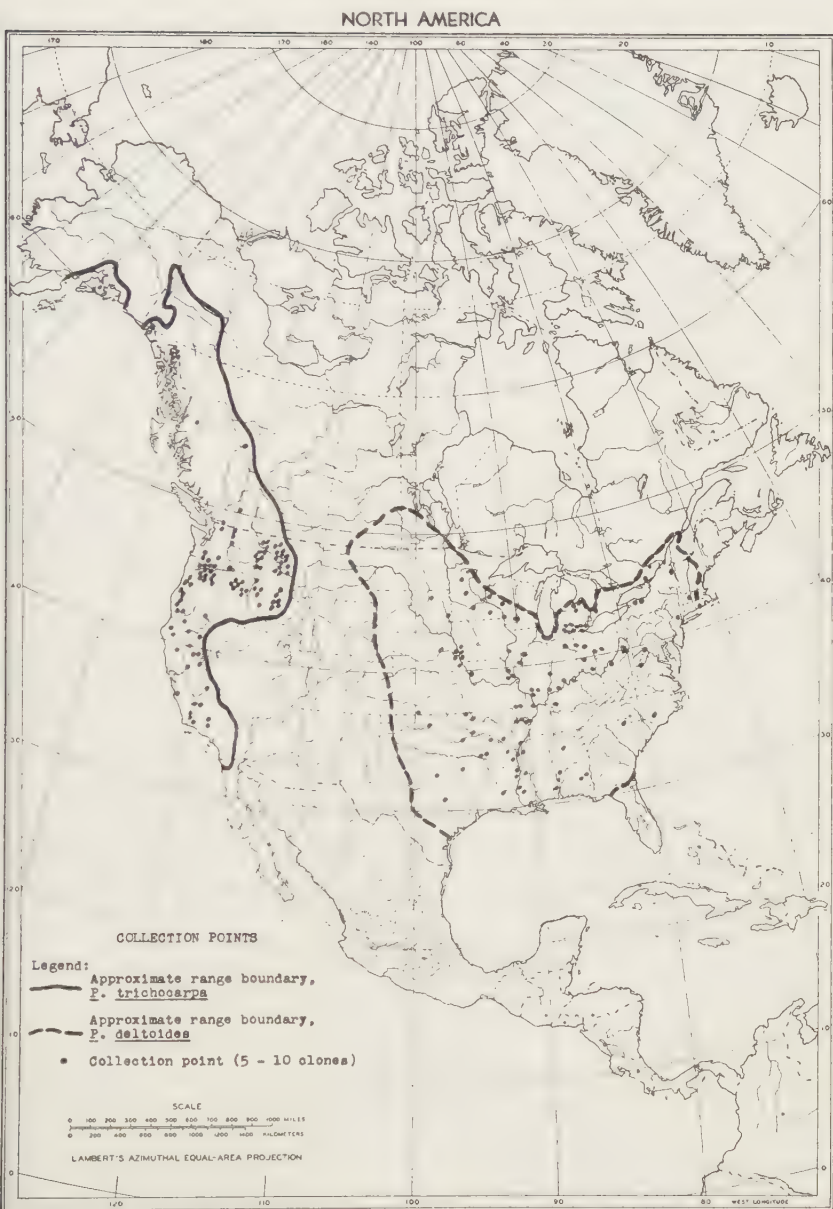


FIG. 1. Approximate ranges of *P. trichocarpa* and *P. deltoides* and collection points for clones used in this study.

Although two such plantations were established in 1950 and 1951, observations at Weston on the date of cessation of height growth for the various clones concerned in this study were all made in the propagation area, hereafter referred to simply as the "Weston area."

The combined experimental facilities of the Arnold Arboretum and the Bussey Institution, located in Jamaica Plain, Massachusetts, a part of greater Boston (ca. 10 miles southeast of Weston), have also been used in this study. The outdoor long-day and normal-day plots used in the 1951 experiments were set out in a portion of the experimental plots used jointly by these institutions, and located on a flat gravelly knoll in the first range of hills south of the Boston basin. The soil, thanks to continuous enrichment and good management, is highly fertile and uniform.

PHOTOPERIODIC RESPONSES IN PLANTS

Biologists, as well as most primitive peoples, have long recognized the indispensable nature of solar energy in the biological scheme. But only within the past thirty years have botanists recognized the notable significance to plant growth and development that is associated with the periodic manner in which this energy is supplied to the earth's surface.

Within the tropical and subtropical regions of the world, there is little change in the length of the daylight period throughout the year; but outside these regions, marked seasonal differences occur. At the latitude of Boston (ca. 42° N.), for example, the length of the daylight period on the shortest day of the year is ca. 9 hours, and on the longest day ca. 15 hours, i.e., a difference of 6 hours (FIG. 2). With increases in latitude the annual variation in day-length is greater. Thus, at the latitude of Juneau, Alaska (ca. 58° N.), day length at the time of the winter solstice is ca. 6.5 hours as compared with ca. 18.5 hours on the day of the summer solstice, a difference of 12 hours. The above day lengths are based on the time of sunrise and sunset. Actually, the effective photoperiods at all latitudes are somewhat greater due to the effects of the morning and evening twilight periods (FIG. 2).

Flowering Response

The response in growth and development exhibited by plants in relation to the length of the daily light period (i.e., *photoperiod*) is called *photoperiodism*. The earlier and, indeed, most of the later investigations concerned with this phenomenon have centered on the flowering response of various herbaceous plant species and varieties when exposed to photoperiods of varying length.

First recognition of the influence of day length on reproductive development in plants was made by Garner and Allard (3) in 1920. These workers observed that Maryland Mammoth tobacco, which normally does not flower in the field during the summer season at the latitude of Washington, D. C. did, nevertheless, flower profusely when grown in a green-

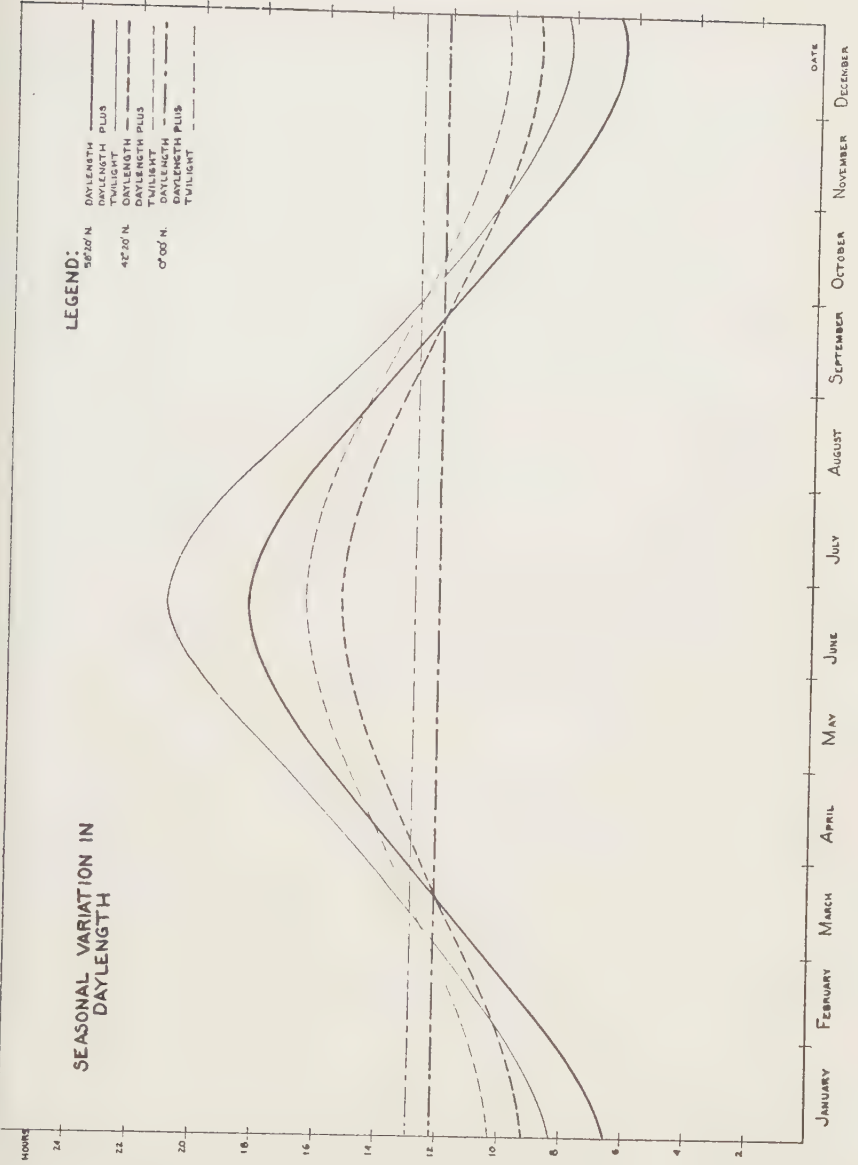


FIG. 2. Seasonal variation in day length at various latitudes: equator, 42° 20' N. and 58° 20' N.

house at the same latitude during the winter. The dissimilar reproductive development observed led to the hypothesis that day length was a controlling environmental factor, the relatively short photoperiods of winter apparently favoring flower production in this variety. Subsequent confirmation of this hypothesis was made through the use of carefully controlled experiments by these and numerous other workers.

The significance of the photoperiodic influence on flowering is obviously a matter of much practical concern in the case of cultivated crops grown for their fruit or seeds. Many of the grains, for example, require long days to flower, and for this reason long-day varieties cannot be successfully moved to southern latitudes. Other long-day plants grown for the food stored in their vegetative organs, such as spinach, lettuce, and radish, must be grown as spring or autumn crops in regions where the long days of summer would otherwise cause them to "bolt."

In order for such short-day plants as the Biloxi soy bean and numerous ornamentals (cosmos, aster, chrysanthemum, etc.) to flower, they must be grown either in the low latitudes or in the short days of spring or autumn in the higher latitudes. Many short-day ornamentals native of the tropics are, of course, grown successfully in greenhouses under the short-day regime of the winter months in northern latitudes.

Plants indeterminate with respect to their photoperiodic requirements for flowering, such as tomato, cotton, buckwheat, and sunflower, may be grown successfully over a wide range of latitudes.

Vegetative Response

Although major interest in the photoperiodic studies involving herbaceous plants has centered on the influence of day length upon reproductive development, most workers have also noted marked effects on vegetative growth as well. Most plants exhibit much better vegetative development when exposed to long photoperiods than to short ones, regardless of the fact that they may be classified as "short-" or "long-day" types with respect to flowering. Maryland Mammoth tobacco, for example, when grown under the long days of summer at the latitude of Washington, D. C., by Garner and Allard (3), attained heights of 10-15 feet; whereas, when greenhouse grown in the short days of winter, it did not exceed five feet.

Conversely, movement of long- or short-day flowering types into natural or artificially created shorter days usually results in marked reduction in vegetative development.

Photoperiodic studies of woody plants have for the most part involved seedlings, and consequently little is known of the influence of day length on reproductiveness. These investigations have, however, demonstrated that variation in day length is a factor of marked importance in the annual vegetative growth cycle of many woody species, particularly as it relates to the control exerted over the timing of physiological processes concerned in the onset of dormancy.

In common with techniques used in the investigation of photoperiodic

responses in herbs, studies of woody plants have involved the testing of various species in a day-length regime different from that prevailing in their native habitat. Whether such tests have involved actual movement of the plants north or south into a new natural day-length pattern, or if short or long days have been artificially created at any particular latitude, the results have been the same. In general, movement from the latitude of the natural habitat northward (i.e., into longer days) prolongs the active period of growth; and movement southward (i.e., into shorter days) shortens it. Such modifications in the length of the active growth period normally result in marked differences in total seasonal increment and frost hardiness. Thus, movement of plants into a day-length regime longer than that of the native habitat characteristically gives increased height growth accompanied by decreased resistance to early autumnal frosts; whereas movement into a short-day regime results in dwarfing, associated with increased frost resistance.

Similar photoperiodic growth responses have been, with but few exceptions, demonstrated by Moshkov (12, 13, 14) and Bogdanov (1) to characterize the behavior of various species in the following genera: *Acer*, *Aesculus*, *Ailanthus*, *Alnus*, *Caragana*, *Corylus*, *Fraxinus*, *Juglans*, *Larix*, *Phellodendron*, *Pinus*, *Prunus*, *Rhus*, *Robinia*, and *Ulmus*; by Kramer (8) and Jester and Kramer (6) in North American species of the following genera: *Acer*, *Fraxinus*, *Fagus*, *Robinia*, *Liriodendron*, *Liquidambar*, *Quercus*, and *Pinus*; by Sylvéén (18) in the European aspen (*P. tremula*); by Johnsson (7) in *Betula*; by Langlet (9) in Scotch pine; and by Olmsted (15) in sugar maple.

INFLUENCE OF PHOTOPERIOD ON TIME OF HEIGHT GROWTH CESSATION IN *POPULUS*

First suggestions of photoperiodic sensitivity among the clones in the propagation area at Weston appeared during the first (1948) growing season. As a result of early height growth cessation and consequent dwarfing, *P. trichocarpa* ecotypes from high latitudes stood out in sharp contrast to those of more southerly origin.

Interclonal Responses to a Uniform Day Length

Precise measurements of height increment by the use of auxanometers of various design have been made by several workers. By their use the time of terminal growth cessation could doubtless be pinned down to a certain hour, or at least to a particular day. Such methods are not, however, practical for the measurement of large numbers of individuals in the field, since the cost would be prohibitive.

In the present studies total height measurements were taken to the nearest centimeter at 7-day, 5-day or 3-day intervals by direct measurement with meter sticks or tapes. Although lacking a high degree of precision, the technique is sufficiently accurate for determining comparative

differences in growth cessation which are spread over a period of several weeks or months. The error occurs during the period immediately preceding the time of actual height growth cessation. The increments between measurements during this period may be so small that the actual day of growth cessation is indeterminable. Depending upon the interval between measurements and other variables, deviations in the date of recorded growth cessation probably vary in the order of 3 to 7 days before and after the actual date of growth cessation. In general this method tends to encourage a later recording of growth cessation.

First systematic recording of the time of height growth cessation in the *Populus* collections was made during the 1950 season in the propagation area at Weston. Relatively small samples of *tacamahaca* and *deltoides* clones were included in the study, the majority being *trichocarpa*. All were derived from cuttings which had been planted in the spring of 1948 or 1949 and were thus in their second or third growing season. Measurements of total height for each of the clones included in the study were taken at weekly intervals from June 27 to November 7.

Active terminal growth in the group of *tacamahaca* clones measured was observed to occur over a period of about 158 days (April 14 to September 19); in the *deltoides* clones over a period of about 178 days (April 20 to October 15); and in the *trichocarpa* group over a period of about 197 days (April 14 to October 28). Although the first killing frost of autumn at Weston occurred the night of September 24–25, the growing season was by no means ended. Plants still in active height growth at that time (*deltoides* and *trichocarpa* of southern origin) suffered some damage to the young unfolding leaves near the growing point, but continued in active height growth thereafter. Subsequent light frosts in October (on the 6th, 8th, 16th, and 21st) caused similar damage; but height growth persisted in some clones until the first heavy frosts of October 26 and 27. These frosts were apparently of sufficient severity to kill all meristematic tissue in the growing points of the plants still active at that time.

The recorded dates of height growth cessation for the various *tacamahaca* clonal lines ranged from about June 20¹ to September 19, a period of 91 days, representing 58 percent of the growing season. Among the *deltoides* group, cessation of height growth occurred between August 15 and October 18, a period of 64 days, or 31 percent of the growing season. The time of height growth cessation in the *trichocarpa* clones was considerably more widespread: first terminal growth cessation was recorded about June 20,¹ and the last on October 28, a period of 130 days, or about two-thirds of the growing season.

Since this considerable intraspecific diversity in time of terminal growth cessation occurred under the essentially uniform environment prevailing in the propagation area at Weston, the conclusion is inevitable that the vari-

¹ Measurements were started on June 27. This date proved too late to record the cessation of height growth of certain *tacamahaca* and *trichocarpa* clones of high latitude origin. Subsequent observations in 1951, 1952, and 1953 have confirmed that height growth in these clones stops ca. June 20.

ous clones within the species observed are genetically diverse in this character. That this diversity is not randomly distributed throughout the range of each species, but is inversely correlated with latitudinal distribution, is revealed by the scatter diagrams that result when latitude of origin for each clone of each species is plotted over the corresponding date on which height growth ceased at Weston (Figs. 3, 4 and 5). The correlation coefficients for these diagrams are all high ($r = -.893$, $-.706$, and $-.823$ respectively), and all exceed the 1 percent level of significance.

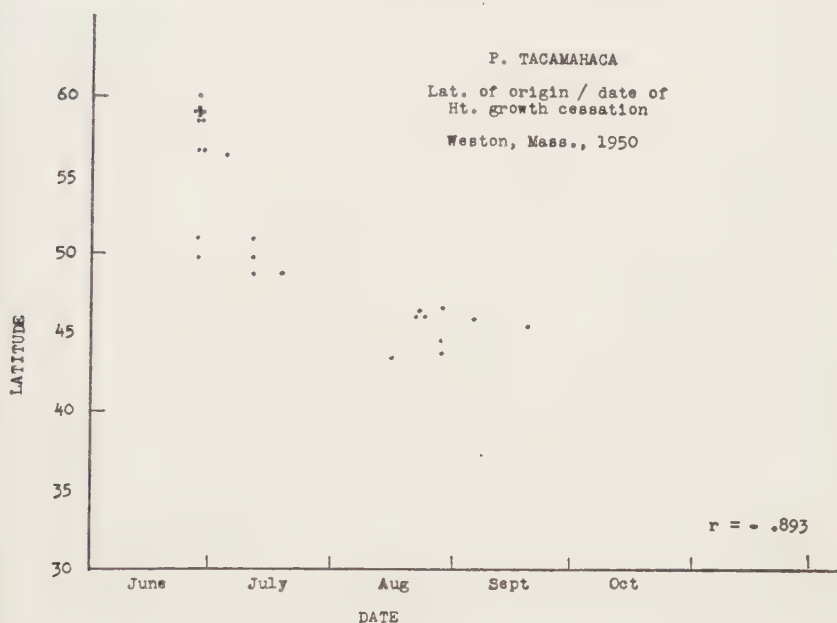


FIG. 3.

The trend of the gradient revealed by these diagrams clearly indicates a tendency for clones of high latitude (long-day) origin to cease terminal growth early, and clones of low latitude (short-day) origin to stop terminal growth late when grown under the mid-latitude day-length regime prevailing at Weston. These results are in agreement with the photoperiodic growth reactions which characterize the behavior of European aspen (Sylvén, 18) and species in other genera when subjected to day-length regimes differing from those in their native habitats. As previously pointed out, various workers have demonstrated that the movement of plants from native habitats of long day into short day is normally characterized by earlier height growth cessation; whereas movement from short day into long day results in delayed growth cessation. As a working hypothesis it therefore appears tenable to conclude that the inverse correlation between latitude of origin and time of terminal growth cessation for the ecotypes

of the *Populus* species here concerned is the result of similar photoperiodic reactions between the various genotypes of the ecotypes represented and the uniform day-length regime to which each was exposed at Weston.

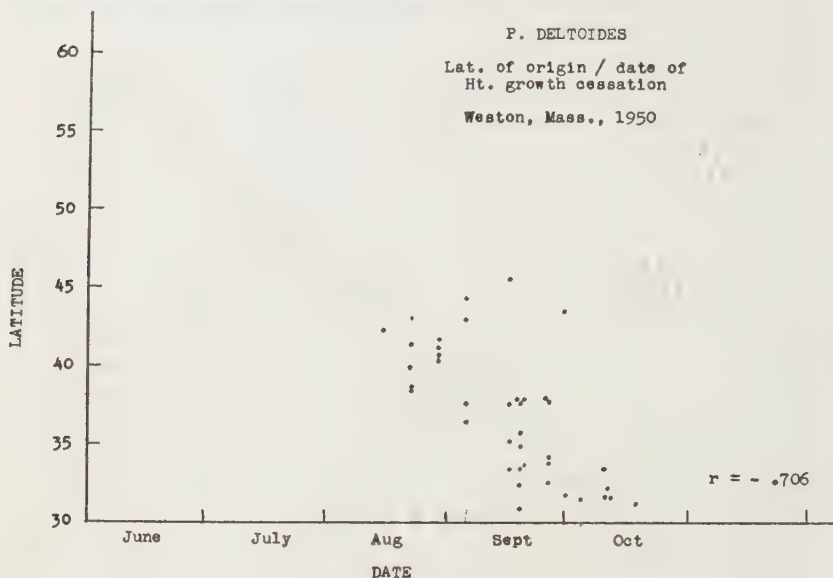


FIG. 4.

Although the clinal nature of the variation is sufficiently well-defined in these diagrams to support the above hypothesis, there is ample evidence to suggest that the relationship between time of height growth cessation at Weston and latitude of origin of the various clones is not necessarily simple and direct. The spread in dates of growth cessation from mid-July to late October among the *trichocarpa* clones native of latitudes between 40° and 50° (FIG. 5), for example, indicates that a pronounced local diversity in photoperiodic response exists, apparently quite independent of latitudinal origin.

That diversity in photoperiodic response may occur locally within a species population under essentially uniform day-length conditions leads to interesting speculation. There can be little doubt, in the first place, that height growth cessation in *Populus* signals the onset of initial physiological processes culminating in winter dormancy. The time during the growing season at which terminal growth cessation occurs thus assumes a role of critical survival value. Through the selective pressure exerted by the first killing frosts of autumn, only those genotypes capable of terminating height growth at a sufficiently early date to escape such frosts are capable of survival. Within any uniform day-length zone, therefore, where the growing season varies considerably in length, due to topography or other factors, the hypothesis may be made that adaptation to any particular

length of growing season is effected through the selection of those genotypes having a suitable photoperiodic response to the prevailing day-length regime of that latitude.

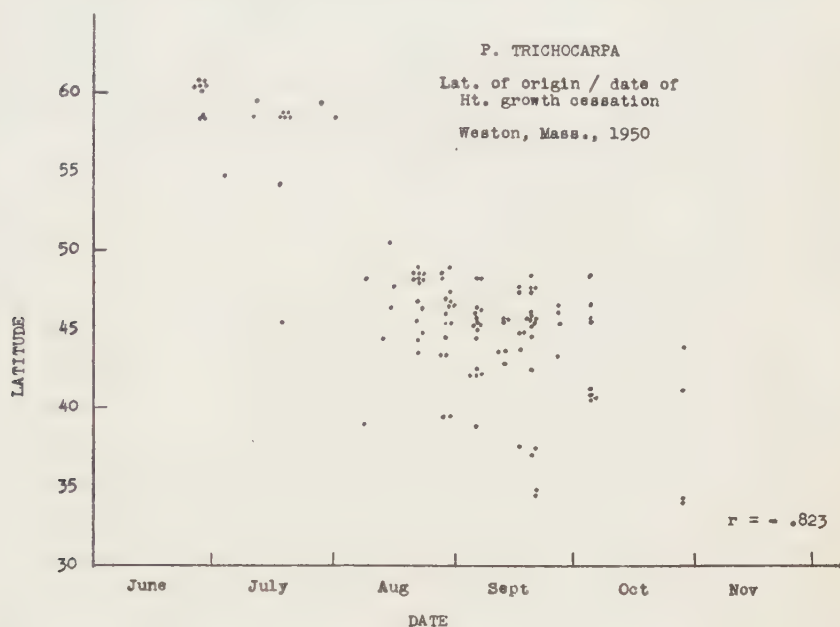


FIG. 5.

The group of clones originating between 40° and 50° (FIG. 5), referred to above, represents a case in point. This group is actually composed of a broad longitudinal sampling of *trichocarpa* ecotypes, extending from the Pacific coast to western Montana, and with a vertical dispersion from near sea level to ca. 5000 feet elevation. Since the length of the frost-free season in this latitudinal zone is, in fact, known to vary widely within comparatively short distances, due to elevation, the nature of the topography, etc., the considerable diversity in time of height growth cessation for clones native of the zone might be satisfactorily explained on the basis of the above hypothesis.

A direct test of the hypothesis may, of course, be made by determining the degree of correlation, if any, that may exist between the lengths of the growing season at the points of origin for clones native of a narrower latitudinal band (i.e., having an essentially uniform seasonal day-length regime) and the dates of height growth cessation for the same clones as recorded at Weston.

Although precise data on the average length of the growing season for the native habitats of each of the clones represented in our collections is for obvious reasons unavailable, reliable estimates nevertheless can be

made for those native to areas in the vicinity of U.S. Weather Bureau Stations (21).

FIGURE 6 shows the scatter diagram resulting when the length of the average growing season for those clones native only of the 2° latitudinal zone (45° to 47°) is plotted over the date of height growth cessation at Weston. The regression path here defined appears sufficiently uniform in trend ($r = +.789^1$) to confirm further the hypothesis that *trichocarpa* populations are capable of adaptation to growing seasons of varying length within uniform day-length zones by selection of those types having a suitable photoperiodic response.

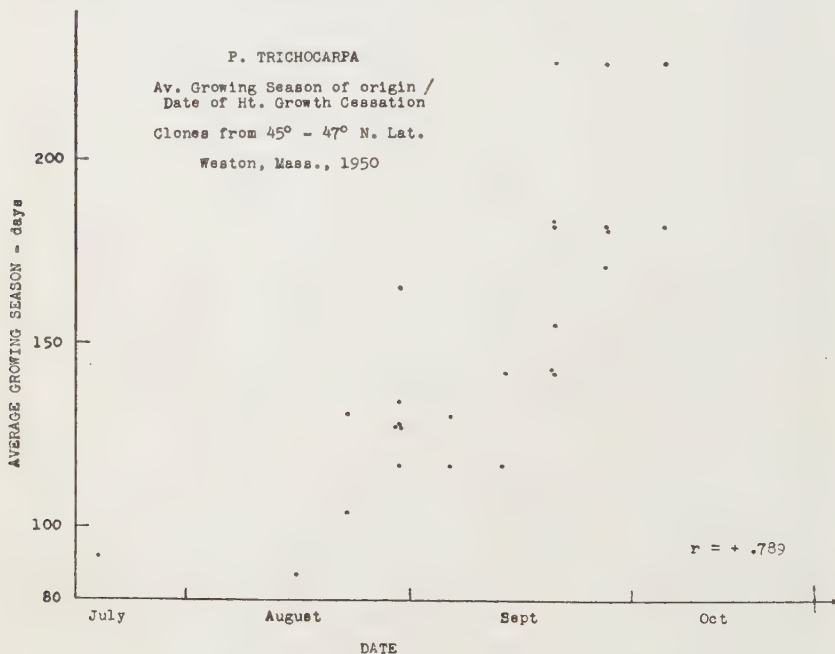


FIG. 6.

Intraclonal Responses to Diverse Day-length Patterns

During the 1950 and 1951 seasons, tests of photoperiodic sensitivity as revealed by influence on time of height growth cessation were made in about 100 clonal lines within the following species: *P. trichocarpa*, *P. tacamahaca*, *P. angustifolia*, *P. deltoides*, and various hybrids of *P. tremuloides* \times *P. tremula*. The tests of 1950 were made in a greenhouse at the Arnold Arboretum with potted propagules of 45 clonal lines grown under short-, normal- and long-day photoperiods. Results of these observations have been previously published (Hoffmann, 4).

¹ Exceeds the 1 percent level of significance.

Similar tests of the same clonal lines, and about 55 additional, were made outside during the 1951 season in portions of the Bussey Institution nursery. Ramets of the various clones in these studies were exposed only to the natural-day pattern prevailing at the latitude of Boston (ca. $42^{\circ} 20'$ N.) and a long-day regime corresponding to that at Juneau, Alaska (ca. $58^{\circ} 20'$ N.).

Flood lights and reflectors for the long-day plot were so arranged as to obtain complete coverage of the area with a minimum ground surface light intensity of 1.5 foot candles. Since the work of Withrow and Benedict (22), Matzke (10), and others demonstrates that light intensities of less than 1 foot candle are capable of producing photoperiodic responses, twice the duration of civil twilight was added to the "sunrise to sunset" day length (FIG. 2). According to Humphreys (5), light intensity at the beginning of civil twilight (morning sun 6° below the horizon) is 0.4 foot candle with a clear sky, and quickly rises above 1 foot candle.

Supplemental light was supplied the long-day plot by means of an automatic time switch in the morning and evening. Adjustment of the switch settings was made every third day to conform to the natural day at Juneau. Use of the lights was discontinued on September 30, when the photoperiod of Boston became greater than that of Juneau. Thereafter both experimental plots received the normal day length of Boston.

The variable responses in terms of height growth cessation to different day-length regimes that were observed added further confirmation of the presumed photoperiodic sensitivity in *Populus*, and also demonstrated the apparent similarity of this response to that exhibited by other tree genera of the temperate zone.

Detailed tabulation of the data recorded in these studies cannot, in the interest of brevity, be included in the present paper. However, a sample of the records on height growth cessation for *P. trichocarpa* clones of various origins when grown under the normal Boston-day and the artificial long-day regimes at the Arnold Arboretum during the 1951 season are shown in TABLE 1 (Columns 7 and 8). Differences in time of growth cessation are noted in Column 9. Included also are recorded dates of height growth cessation of the same clones under normal-day conditions at Weston in 1950 and 1951 (Columns 5 and 6).

As these data indicate, diversity of intra-clonal response to normal- and long-day regimes was most pronounced in those clones (981 and 984) from high latitude habitats. The net phenotypic disparity in height and leaf development between ramets of such northern clones when grown in the long-day regime to which they are adapted and the shorter-day regime of Boston is most striking (FIG. 7).

Similarly, marked intra-clonal differences in time of height growth cessation characterize those clones adapted to the high-elevation (short growing season) habitats in the lower latitudes when grown in the normal- and long-day regimes (clones 1047, 1485, and 1239, TABLE 1). In contrast, intraclonal diversity in response to normal- and long-day photoperiods demonstrated by those clones originating in the low-elevation (long grow-

ing season) habitats of the lower latitudes is characteristically small (clones 895, 899, 825, and 957, TABLE 1).

TABLE 1

TIME OF HEIGHT GROWTH CESSATION IN NORMAL- AND LONG-DAY REGIMES
P. trichocarpa

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Clone No.	Origin			Date of Ht. Growth Cessation				Difference (days) (8)–(7)
				Normal Day		Long Day		
	Weston		Arn. Arb.	Arn. Arb.				
	1950	1951	1951	1951				
981	60–37	149–30	1300		6/25	6/20	8/28	69
984	60–19	149–21		... ¹	6/19	6/20	8/19	60
1147	48–30	115–55	1850	8/29	8/28	8/28	10/3	36
1151	48–25	114–30	2100	8/29	8/28	9/12	9/27	15
1565	48–10	114–10	8000	8/1	7/31	8/28	9/27	30
1029	47–30	123–55	250	9/19		9/21	10/5	14
1047	47–35	115–25	2400	9/12		8/29	9/28	30
895	46–10	122–55	30	9/26	9/18	10/3	10/12	9
1485	46–20	112–15	5000	8/15	8/7	8/10	9/13	34
899	45–35	122–35	25	9/26	9/18	10/7	10/12	5
1324	45–15	117–45	3400	9/5	8/28	9/18	10/3	15
825	44–30	123–25	200	9/19	9/18	10/5	10/11	6
1239	44–30	114–15	5200	8/29	8/28	8/31	10/3	33
957	43–25	123–25	500	9/26	9/18	10/6	10/11	5
1137	43–35	114–25	5300	8/29	8/28	8/31	9/27	27

¹ Height growth cessation occurred prior to June 27, 1950.

A point of considerable physiological interest is suggested by the results of the normal- and long-day tests. Theoretically, the net superiority in height shown by ramets of those clones grown in the long-day environment may be attributable to the combined influence of two causes: (1) the longer *season* of growth; and (2) the longer *daily* light period. Although the tests were not designed to analyze quantitative growth differences, the available data suggest that the longer daily light period did not materially contribute to the net seasonal height increment of plants grown in the long day. The superiority in the height of plants given the long-day treatment appears, thus, to have resulted solely from their longer growing season.

Other Environmental Factors Influencing Time of Height Growth Cessation

In general, little disparity was noted in the time of height growth cessation among ramets of the various clones when grown under the influence of the same day-length regime during the same or even succeeding seasons

(TABLE 1). Most minor fluctuations (1 to 10 days) may doubtless be attributed to inaccuracies inherent in the measurement technique employed. Others, demonstrating fluctuations of a higher order, such as the 21-day difference in date of height growth cessation of clone 1324 (TABLE 1) as recorded at Weston and the Arnold Arboretum in 1951, suggest the modifying influence of other factors on the photoperiodic reaction.



FIG. 7. Diversity in phenotype demonstrated by ramets of *P. trichocarpa* clone No. 984 when grown in the normal day-length regime of Boston (left); and in an artificially created long-day regime approximating that of its native Alaskan habitat (right). Height growth ceased in the ramet exposed to Boston day length on June 20, 1951; that exposed to the long-day regime stopped growth 60 days later (August 19, 1951). Scale is in feet.

That other environmental factors should serve to modify the photoperiodic response is by no means unusual. Among the factors most suspect is temperature. Garner and Allard (3) observed modification in the photoperiodic requirement for soy beans when grown in different temperatures, and similar reports have been made by other workers (Roberts and Struckmeyer, 17; and Parker and Borthwick, 16). Since most differences in time of height growth cessation between ramets of the same clone

grown at Weston and the Arnold Arboretum were due to earlier cessation of growth at Weston, the uniformly lower temperatures of that locality may have been responsible. (Differences in the natural day length of the two localities is negligible, since they are separated by only ca. 2 minutes of latitude.)

On the basis of experiments currently in progress, there is evidence that ramets of a clone grown in sod may be induced to stop height growth at an earlier date than those grown in cleanly cultivated soil.

There is some indication that excesses of available nitrogen in the soil (Kramer, 8) delay the onset of dormancy in apple trees, and this factor may thus influence time of height growth cessation.

In addition to the above factors, the quite empirical conclusion may be drawn that an apparent intraclonal diversity in physiological functions may frequently develop among ramets of a clone. Such differences appear to be associated with mechanical injury or attack by disease or insects.

ROLE OF THE PHOTOPERIODIC RESPONSE IN THE ANNUAL GROWTH CYCLE OF *POPULUS* SPECIES

Break of Dormancy and Early Seasonal Growth

Although light exerts a profound influence on growth activity during a large portion of the growing season in *Populus*, neither light nor its periodicity appears to be directly concerned in the break of dormancy.

In the propagation area at Weston, marked intra- and interspecific differences in time of leaf flushing are annually observable in early spring; but preliminary results of forcing studies made in 1950, 1951, and 1952 indicated that such differences reflect a diversity in response to prevailing temperatures, apparently acting quite independently of the light environment. In order to test more adequately for a possible light influence on dormancy break, ramets of various clones and sibs of several progenies representing species in all sections of *Populus* were grown in continuous light, natural day, and continuous darkness for a period of ca. three months in the late winter and early spring of 1953. The three compartments were maintained at as uniform a temperature as the facilities available permitted (ca. 70° F.).

Significantly, break of dormancy was negotiated without apparent incident by all plants in the dark compartment.¹ Within those clones and seedling families which broke dormancy early, little disparity (0-2 days) in date of dormancy break between compartments was noted. Within the late-breaking clones and seedling families, there were, however, marked divergencies (3-9 days); but there was no indication that complete ab-

¹ So-called "break of dormancy" in these studies was based on observed separation of bud scales. As *Populus* buds swell, the imbricate bud scales separate, revealing the transparent portion of the underlying scale. Examination of the plants in the dark compartment was effected by use of weak yellow light which, in addition to the green portion of the spectrum, is reported to be photoperiodically ineffective, at least in the flowering response (Miller, 11).

sence of light was more inhibiting to the break of dormancy than continuous light.

Date of appearance of the first unrolled leaf was also recorded in these studies. In most cases the flattening process was not complete in the plants subjected to the dark treatment.

Subsequent growth of the plants in darkness gave rise to the typical morphological modifications associated with etiolation, i.e., reduction in leaf size, marked elongation of the shoot with the development of a hook at the end, inhibited diametral growth, and loss of the erect habit (Fig. 8).

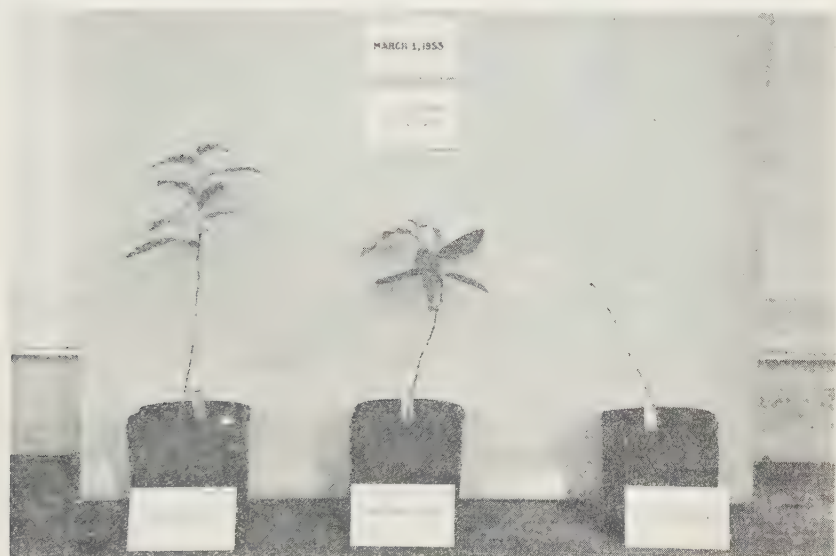


FIG. 8. 1-year seedlings of *P. trichocarpa* grown for 5 weeks in normal day (left); continuous light (center); and continuous darkness (right). All plants were dormant at the start of the experiment and all broke dormancy 8 to 10 days later.

Results of these studies appear to confirm the conclusion that the photoperiod is ineffective in the break of dormancy or early growth in length of *Populus*. Later, however, a stage in the annual growth cycle is reached when the day length must be greater than a certain minimum in order for height growth to continue. As has been demonstrated, high latitude clones of *P. trichocarpa*, when grown in the natural-day regime at the latitude of Boston, cease height growth on or about the time of the summer solstice. If, however, the photoperiod is lengthened by the addition of artificial illumination, they continue to grow, ceasing only when the day length again falls below the critical minimum. The role of the photoperiod in the annual growth cycle of *Populus* thus appears to be primarily effective in the timing of physiological processes concerned in the onset of dormancy.

Diametral Growth Cessation

On the basis of weekly recordings of height and diametral increment made on representatives of various *Populus* species in the plantations at Weston and elsewhere during the 1952 season, it is clear that diametral growth is always terminated after height growth ceases. Interclonal differences in the length of time between height and diametral growth cessation ranged from ca. 10 to 30 days; but there appears to be little evidence from these data to suggest that diametral growth cessation is independently controlled by the photoperiod. A more likely explanation seems to be that cessation of growth in diameter is simply one of the final, and perhaps more or less automatic, steps in the dormancy process.

INHERITANCE OF THE PHOTOPERIODIC RESPONSE

The broad and continuous range in time of height growth cessation which characterizes the behavior of the various ecotypes in these studies, suggests that a large number of genes are involved in the photoperiodic reaction. Further indications of multiple factor inheritance are contained in the records on height growth cessation for the offspring and parents of a north-south cross included in the 1951 studies. Under the influence of either the normal- or long-day regime, the progeny ceased height growth at a time intermediate to that of their parents (Table 2).

TABLE 2

NORTH-SOUTH CROSS
DATE OF HEIGHT GROWTH CESSATION FOR PARENTS (183A \times 118) AND
PROGENY (1599 AND 1600)

Clone No.	Lat. of origin	Date of Height Growth Cessation, 1951	
		Normal-day Plot	Long-day Plot
183A	58-30	8/10	9/15
118	46-50	9/12	10/3
1599		8/25	9/21
1600		8/24	9/20

PRACTICAL AND THEORETICAL SIGNIFICANCE OF THE PHOTOPERIODIC GROWTH RESPONSE

Seed Source

Although it would be unwise on the basis of our present limited knowledge to extend the results of these studies to all ligneous species, several practical generalizations concerning the photoperiodic response in trees and its importance in seed source problems may be noted.

- (1) The utilization of seed from northern long-day races for planting in

southern latitudes of long growing season will result in early seasonal growth cessation and consequent dwarfing. Such seed sources should obviously be avoided for the establishment of forest plantations from which maximum production of wood or fiber is desired. On the other hand, such seed sources might prove suitable for the establishment of protection forests in short growing season habitats at high elevations in southern latitudes. The typically small annual increment of northern races when grown in a short-day environment might even make them suitable for special horticultural uses.

(2) Seed derived from ecotypes native of the short growing season, high-altitude habitats of mountainous areas in the low latitudes may be expected to react in a manner similar to northern long-day types and should therefore be avoided as seed sources for forest plantations at the same or more southern latitudes. Such sources of seed may, however, prove highly desirable for introduction into certain long-day environments in northern latitudes having suitably long growing seasons. Support for this generalization is attested by the long history of successful North American tree introductions into the maritime countries of Europe. Conversely, movement of long-day races of native European species into the United States has not met with notable success.

(3) Ecotypes native of long growing season habitats in any particular latitude should be avoided as seed sources for short season habitats at the same latitude because of their susceptibility to early autumn frost damage. For the same reason, such seed sources cannot be successfully moved northward into a long-day environment.

The problem of selecting suitable seed sources of any species for introduction into another environment must obviously take into consideration numerous other environmental factors and genetic characteristics. The above recommendations may be found useful, therefore, only to the extent that they may contribute to limiting the field of search for desirable genotypes. Final decisions on adaptability of the proposed introduction to the new habitat must be based on the observed interaction that results between the introduced genotype and all the factors of its new environment.

Breeding

Because of its fundamental role in the vegetative growth cycle, the photoperiodic response should obviously be a matter of primary concern to the tree breeder. As a means of increasing the net yields of wood or fiber, gene combinations nicely adapted for full utilization of the growing season in a particular habitat, may well prove to be quite as promising as a search for heterotic hybrids.

In view of the probably high genetic diversity of the photoperiodic response in wild tree populations occupying a wide diversity of habitats, initial concern should be directed to the selection of suitable parental materials. This is especially true in F_1 breeding programs and may, to a large extent, explain the unsatisfactory results that have been obtained

by various workers through the selection of parental stocks based on their taxonomic identity and availability, rather than their genetic quality.

Since the photoperiodic response appears to be controlled by a large number of factors, the production of a wide-ranging, transgressive series of photoperiodic types may be expected in F_2 populations. Theoretically, by the initial use of parental ecotypes which give reactions approaching the extremes in day-length response, an F_2 will result which may be expected to contain gene combinations adaptable to almost any growing season length at any latitude.

SUMMARY

For the purpose of studying ecotypic variation in *Populus*, a living collection representative of the ranges of various species in this genus was undertaken in 1947 by the Maria Moors Cabot Foundation for Botanical Research. The studies here reported are concerned primarily with the influence of the photoperiod on time of height growth cessation as observed in the various test areas located in the vicinity of Boston, Massachusetts.

Marked variation in the time that height growth stopped was observed between clonal lines of single species when grown in the same day-length regime and otherwise uniform environment. Analysis of these data revealed that the time of height growth cessation was inversely correlated with the latitude of origin of each clone. Among clones native of uniform day-length zones, the time at which height growth ceased was directly correlated with the length of the frost-free season prevailing in the native habitat of each clone. On the basis of these observations, the conclusion is made that adaptation of *Populus* species to various habitats differing in length of frost-free season is effected by a genetic mechanism which controls the duration of their seasonal period of growth. The photoperiod, which is the only factor of the environment with a uniform seasonal variation that is constant from year to year, functions as the timing device for this mechanism.

Modifications in time of height growth cessation were effected by exposing ramets of various clones to artificially lengthened or shortened photoperiods in otherwise uniform environments. The time of height growth cessation was thus demonstrated to be the result of an interaction between the individual's genotype and the photoperiod. Also observed were other intraclonal modifications in time of height growth cessation that could not be attributed to photoperiodic response. Differences in temperature, available nitrogen, intensity of cultivation, and various other factors are believed to exert a modifying influence on the time that height growth ceases.

Hybrids between clones of northern and southern origin gave a photoperiodic response intermediate to the responses of the parents. These results, and the widely varying photoperiodic responses shown by the various ecotypes used in these studies, indicate that the number of genes involved in the photoperiodic reaction is large.

Experiments on the break of dormancy in the spring indicated that temperature rather than photoperiod is the major factor controlling the initiation of new growth after the period of winter dormancy.

Several practical generalizations concerning the photoperiodic response in trees and its importance in seed source problems and in breeding are noted.

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NOTES ON THE FLORA OF CHINA, III

SHIU-YING HU

With two plates

CRITICAL NOTES on ambiguous binomials concerning the Chinese flora, additional information regarding certain Chinese plants, and the proposal of eight new species, four new varieties, and two new combinations are presented in this paper. Unless identified by (G), indicating that the material is deposited in the Gray Herbarium, all the specimens cited are to be found in the Herbarium of the Arnold Arboretum.

***Clematis angustifolia* Auct.**

Jacquin in 1762¹ published the species *Clematis angustifolia*, from the coast of southern Europe. According to his description the species was a glabrous vine with pinnate leaves and linear leaflets. Pallas in 1776 described *Clematis hexapetala*, an erect plant with tomentose perianth from eastern Siberia in the regions of the Argun and Onon Rivers. In 1786 Jacquin, probably on account of the shape of the leaf segments, doubtfully amalgamated these geographically widely separated and morphologically manifestly different species. In the discussion of his *Clematis angustifolia* he wrote as follows, expressing his doubt: "An haec eadem cum Ammaniana planta, a Pallasio citata, sit, dubito, quum nostra sit glabra tota, Ammanius vero dicat caules superius lanuginosos . . ." In the same year, under the name *Clematis angustifolia*, he published a colored plate illustrating a plant which he described as erect and with pinnate recurved leaves and linear-lanceolate leaflets. Judging from this illustration and description, Jacquin's concept of his own *Clematis angustifolia* had, by this time, changed from a climbing glabrous vine growing on the coast of southern Europe to an erect pubescent plant occurring in the mountains of central Siberia, for in the Gray Herbarium there is a specimen collected by Schschukin in Irkutsk which matches Jacquin's illustration in every respect. This illustration of Jacquin's has been very misleading, for in the last two centuries botanists who named plants by matching them with illustrations have identified all members of that heterogeneous group of erect herbaceous perennial *Clematis* from North China, Manchuria, Korea, and Eastern Siberia as *Clematis angustifolia* Jacq. Meanwhile most authors who have published accounts of the flora of eastern and northeastern Asia have indiscriminately applied such identifications. Now, both in the herbaria and the literature, we have this oriental taxon carrying an occidental binomial. As Jacquin's species was first published as a climbing

¹ Enumeratio Stirpium Plerarumque, quae Sponte Crescunt in Agro Vindobonensi, Montibusque Confinibus 310.

plant growing on the coast of southern Europe, the application of that binomial should be limited to plants of that region, in spite of the fact that Jacquin later changed the concept of his species. A. P. De Candolle in 1817 (*Regni Vegetabilis Systema Naturelle* 134, 154) treated *Clematis maritima* Linn. as a variety of *Clematis flammula* Linn. var. *maritima* (L.) DC. in one place and later used it again as a synonym of *Clematis angustifolia* Jacq. In so doing, he seems to have given us a hint that Jacquin's original *Clematis angustifolia* might have been a *Clematis flammula* Linn. var. *maritima* DC., since *Clematis flammula* Linn. is a vine with pinnatisect leaves, and the variety, *C. flammula* Linn. var. *maritima* (L.) DC., has linear segments. This vine habit and the pinnatisect leaves with linear segments are distinguishing characters which Jacquin at first ascribed to his *C. angustifolia*. In the herbarium of the Arnold Arboretum there is a collection from Yeste, Spain, labeled *C. flammula* Linn. var. *maritima* (L.) DC. This specimen represents a glabrous vine with pinnatisect leaves. The linear segments of these leaves appear similar to those of some form of the Chinese elements. It is very likely that this represents the true *C. angustifolia* Jacq., which is very different from the taxon of northeastern Asia, which should be designated as *Clematis hexapetala* Pallas.

Hayata in 1913 overlooked Jacquin's binomial and published a *Clematis angustifolia* from Formosa. This species was originally described as *Clematis leschenaultiana* DC. var. *angustifolia* Hayata in *Jour. Coll. Sci. Univ. Tokyo* 30: 16. 1911. It represents a vine with densely tomentose stems and leaves. The leaves are trifoliate with ovate or oblong-lanceolate leaflets which are remotely serrate. The achenes of this species are fusiform. *Clematis leschenaultiana* DC. was originally described from Java. It has been recorded from the Philippines, Formosa, and the warmer regions of the Chinese mainland, as well as from the western Malaysian area. After comparing specimens collected within this wide range I have decided that the Formosan material is not specifically distinct.

Clematis hexapetala Pallas, *Reise* 3: 735, *pl. Q, fig. 2*. 1776, et *Voy.* 4: 701, *pl. 14, fig. 3*. 1793. — Komarov & Schischkin, *Fl. URSS* 7: 318. 1937. — Kitagawa, *Lin. Fl. Mansh.* 217. 1939. — Nakai in *Jour. Jap. Bot.* 20: 191. 1944.

Clematis angustifolia Jacq., *Ik. Pl. Rar.* 1: 11, *pl. 104*. 1786 (non Jacq. 1762). — DC., *Syst.* 1: 153. 1817, et *Prodr.* 1: 7.1824. — Bunge in *Mém. Div. Sav. Acad. Sci. St. Pétersb.* 2: 75 (*Enum. Pl. Chin. Bot.*). 1833. — Ledeb., *Fl. Ross.* 1: 2. 1841. — Maxim. in *Mém. Div. Sav. Acad. Sci. St. Pétersb.* 9: 468 (*Ind. Fl. Pekin.*). 1859, et *Enum. Pl. Mongol.* 2. 1889. — Franch. in *Nouv. Arch. Mus. Paris* II. 5: 166 (*Pl. David* 1: 14). 1882. — Hemsl. in *Jour. Linn. Soc. Bot.* 23: 2. 1886. — Nakai in *Jour. Coll. Sci. Univ. Tokyo* 26: 11 (*Fl. Kor.* 1: 11). 1909, et 31: 426 (*Fl. Kor.* 2: 426). 1911. — Cowdry in *Jour. Roy. As. Soc. N. China* 53: 160 (*Pl. Peitaiho*). 1922. — Limpricht, *Bot. Reis. Hochgeb. Chin. Ost-Tib.* 374. 1922. — Rehder in *Jour. Arnold Arb.* 4: 185. 1923. — Komarov, [*Fl. Manchzh.*] 2: 288. 1950.

Clematis pallasii Gmel. *Syst.* 873. 1791.

Clematis recta Linn. var. *angustifolia* (Jacq.) Kuntze in Verh. Bot. Brand. 26: 112. 1884.

Clematis angustifolia Jacq. var. *breviloba* Freyn in Oesterr. Bot. Zeit. 45: 59. 1895, et 51: 374. 1901.

Clematis angustifolia Jacq. var. *dissecta* Yabe, Higasi-Moko Syokubutsu Mokuroku 14. 1917.

Clematis angustifolia Jacq. forma *dissecta* (Yabe) Kitagawa in Rep. First Sci. Exped. Manch. IV. 4: 17, 83. 1936.

Clematis hexapetala Pallas forma *dissecta* (Yabe) Kitagawa, Lin. Fl. Mansh. 217. 1939.

Clematis hexapetala Pallas forma *breviloba* (Freyn) Nakai in Jour. Jap. Bot. 20: 191. 1944.

CHINA: Chili [Hopei]: Hsiao-wu-tai shan, *T. N. Meyer* 92; Peking, *S. W. Williams*, Aug. 1876 (G); Hsing-lung shan, *J. C. Liu* 622.

EASTERN SIBERIA AND MANCHURIA: Kirin, *F. H. Chen* 182 (G); Dairen, Chinchou, *P. H. Dorsett & W. J. Morse* 5937 (G); Harbin, *P. H. & J. H. Dorsett* 3292 (G); Nertschinsk [Nerchinsky], *F. Karo* (Plantae Dahuriae) 152c (ISOTYPE of *Clematis angustifolia* Jacq. β *breviloba* Freyn); Blagowjestschensk, *F. Karo* 113b; Chabarovsk [Khabarovsk], *V. Komarov* 706; Khingan-skia, *D. Litvinow* 326, 1015; [Ta-ho-shang shan], *K. Kobayashi*, June 19, 1933; Suifenho, *B. V. Skvortzov*, July 10, 1926; Greater Khingan, Djalautins, *B. V. Skvortzov*, July 27, 1938. Mukden [Moukden], *E. H. Wilson* 8818.

Pallas was the first post-Linnaean botanist who described and illustrated the northeastern Asian erect herbaceous perennial *Clematis* and named it *C. hexapetala*. The leaf of his plant is "per caulem opposita, adscendentia, pinnata: foliolis duris venosis, marginatis, acutis, imi paris ramoso-quadrifidis, superioribus lanceolatis bifidisque, terminali tripartito." The segment of the perianth is "oblonga, extus tomentosa." Plants so characterized had been recorded from Manchuria, northern Korea, and the North China Highlands extending from Long. 108° E. and Lat. 34° N. northeastward to Long. 122° E. and Lat. 40° N. Unfortunately, on account of Jacquin's changed concept of his European species of *C. angustifolia* and his misleading illustration of 1776, this taxon has appeared as *C. angustifolia* Jacq. in botanical literature, especially in that concerning the flora of North China.

Clematis hexapetala Pallas is essentially an upland species growing on grassy mountain slopes. Its distribution is very interesting. So far as our material and records show, it has never been collected west of Long. 103° E. nor south of Lat. 34° N. Its range forms a U-shaped area on the map, with Khabarovsk and northern Korea on the curve, northern Manchuria, Dahuria, and the Lake Baikal area on the northern arm, and with southern Manchuria and the North China Highlands on the southern arm.

The material collected within this range exhibits a definite pattern of variation in the size and shape of the ultimate segment of the pinnatisect leaves. Some of these are linear, measuring up to 5 cm. long and 5 mm. wide in the middle, while others are lanceolate, up to 10 cm. long and 10 mm. or more wide in the middle. Since 1895 many trinomials have been

proposed for the different forms of this variation. Although in the original description the measurements of the ultimate segments of the leaves of typical *C. hexapetala* Pallas were not given, and the type material is not accessible to me for comparison, from Pallas' illustration I am inclined to think that he definitely had a narrow-segmented form with segments 2.5–5 cm. long and 3–5 mm. wide at the middle, and acute at the apex.

When Freyn described his varieties, he stated for *C. angustifolia* Jacq. α *longiloba*, "Die Blätter doppelt gefiedert, mit lineal-lanzettlichen Abschnitten; letztere 8–10 mal länger als breit (4–6–10 mm.). Die Blüten bis 5 cm. im Durchmesser, die jungen Sepalen aussen dickt filzig wollig." For his *C. angustifolia* Jacq. β *breviloba* he gave no measurements but simply added, "wie vorige, aber die Blattabschnitte bei gleicher Breite viel kürzer." Here in the herbarium of the Arnold Arboretum there is an isotype, *F. Karo 152c*, for the latter variety. The size and shape of the ultimate segments of the pinnatisect leaves are identical with those shown in Pallas' illustration. Freyn probably did not realize that Nerchinsky, the locality where *Karo 152c* was collected, lies between the rivers Argun and Onon, the type locality of *C. hexapetala* Pallas. The morphological identity and the geographical coincidence lead me to decide that Freyn's *C. angustifolia* Jacq. β *breviloba* is identical with the typical *C. hexapetala* Pallas. The trinomials proposed by the Japanese botanists have been interpreted as synonyms of *C. angustifolia* Jacq. β *breviloba* Freyn by Nakai. They are here treated as synonyms of *C. hexapetala* Pallas.

Pritzel in 1900 recorded this species under the name of *C. angustifolia* Jacq. from T'ai-pa-shan of southwestern Shensi, as represented by *Giraldi 865*. If his identification is dependable, this collection marks the southernmost limit in the range of distribution for the species. As I have not seen Giraldi's specimen, I am not sure whether it actually belongs here or not.

Clematis hexapetala Pallas var. *longiloba* (Freyn) comb. nov.

Clematis angustifolia Jacq. α *longiloba* Freyn in Oesterr. Bot. Zeit. 45: 59. 1895.

CHINA: Chihli [Chihli, Hopei]: Peking, Western Hills, *P. H. Dorsett & W. J. Morse 7035*; same locality, *Bretschneider* in 1881 (ex Herb. F. B. Forbes 1807); Kiang-hsuai ho, *T. F. King 171*; San-tun-ying, *F. N. Meyer 91*; Hsiao-wu-tai shan, *F. N. Meyer 1352*; same locality, *C. W. Wang 61450*; Wei-chang, *Wm. Purdom 44*; without precise locality, *Father Chanet 28*. Shansi: central part of the province, Lu-yah shan, *H. Smith's collector, Lao Ch'in 8147*.

EASTERN SIBERIA OR MANCHURIA: Zejshaja Pristan am Zeafusse, *F. Karo 334*, July 1899; Blagovesczensk, *F. Karo*, July 16, 1904; Amur, super et medius, *Korsinsky* in 1891 (G); Irkutsk [Irkutsk], *Schschukin* (G); Moukden, *J. Webster* in 1887 (G); Dahuria, *Turczaninow 8*, Nov. 1859 (G).

KOREA: Pyengyan, *Mrs. R. K. Smith*, July 5, 1937.

This variety is characterized by the larger leaf segments, which are 10–15 mm. wide, attenuated at both ends, acute, rarely obtuse at the apex, sparsely villose on the principal nerves, especially beneath, glabrescent

later in the season. This variety has been introduced into cultivation. I have seen material from Jewell Nursery, Lake City, Minnesota, which is identical with our spontaneous collections. In North China the plant grows on grassy slopes along the dry hillsides. Its white flowers appear in June and July. The obovate achenes are 5 mm. long, 3.5 mm. wide, compressed, villose, and with a persistent densely villose curved style up to 3.5 cm. long.

***Clematis hexapetala* Pallas var. *smithiana* var. nov.**

Herba erecta perennis, 20–30 raro usque 60 cm. alta; foliis pinnatisectis, segmentis ultimis lanceolatis, 1.5–3 cm. longis, 3–7 mm. latis, apice obtusis apiculatisque, subtus villosis, inflorescentiis subpaniculatis, perianthiis lanatis, segmentis oblanceolatis, 1 cm. longis, 3 mm. latis, antheris oblongis, 1.5 mm. longis, carpellis albo-villosis.

CHINA: Shansi: Yün-ch'eng, Chung-t'iao shan, *H. Smith* 6039 (TYPE); Huo hsien, *T. Tang* 1010.

This is a dwarf variety which is usually 20–30, rarely up to 60 cm. high at the flowering stage. It can easily be distinguished from all other varieties of this species by its villose lower leaf-surface. It occurs in southern Shansi at an altitude of 1850 meters. The white flower appears in July.

***Clematis hexapetala* Pall. var. *tchefouensis* (Debeaux), comb. nov.**

Clematis angustifolia Jacq. var. *tchefouensis* Debeaux in Act. Soc. Linn. Bordeaux 31: 117 (Fl. Tch'ou-fou 22). 1877.

Clematis angustifolia sensu Faber in Denkschr. Entwickel. Kiautschou 31. 1898. — sensu Rehder in Jour. Arnold Arb. 4: 185. 1923, pro parte, non Jacquin, 1762.

CHINA: Shantung: Tche-fou [Chefoo, Chih-fou, Yen-t'ai], *O. Debeaux* (ISOTYPE of *Clematis angustifolia* Jacq. var. *tchefouensis* Debeaux); Tsingtao, Li-chuan, *C. Y. Chiao* 2979; near coast, *A. Jacot*, July 1, 1927; Lao shan, 33 miles south of Tsingtao, *C. Y. Chiao* 2691.

This variety was originally described on the basis of material collected from the north shore of the Shantung Peninsula. Additional material has proved its rather extensive range, extending to the southern end of the peninsula. It can be distinguished from typical *Clematis hexapetala* Pall. by its subglabrous perianth, which is 2–2.5 cm. in diameter at anthesis.

***Clematis hexapetala* Pall. var. *insularis*, var. nov.**

Herba erecta, caudicibus 1 m. altis, 4 mm. crassis, foliis pinnatisectis, segmentis lobatis vel partitis, ultimo lanceolato, 3–6 cm. longo, 8–13 mm. lato, apice obtuso mucronatoque; floribus subpaniculatis, pedicellis 5–8 cm. longis, perianthiis glabrescentiis, 2.5 cm. diametro.

CHINA: Shantung: Tsingtao, Tsingtao Island, *C. Y. Chiao* 2521 (TYPE).

This erect, herbaceous, broad-segmented variety is endemic to a small island on the southern coast of the Shantung Peninsula, where it grows on sandy slopes at sea level. Its white flowers appear in mid-June. Its leaf-

segments resemble those of *C. hexapetala* Pall. var. *longiloba* (Freyn) S. Y. Hu, but the latter taxon can easily be distinguished by its white lanate perianth and sparsely villose nerves on the lower surface of the leaves, while the perianth of this variety is glabrescent and the leaves entirely glabrous.

***Clematis hexapetala* Pall. var. *elliptica* var. nov.**

Clematis angustifolia sensu Finet & Gagnepain, Contrib. Fl. As. Or. 1: 21. 1905, pro parte. — sensu Loes. in Beih. Bot. Centralbl. 37 (Abt. 2): 112. 1919, non Jacquin, 1862.

Herba erecta perennis; foliis pinnatisectis, praeter nervos subtus glabris, segmento ultimo lanceo-elliptico, 1.5–3 raro usque 5 cm. longo, 4–5 raro usque 8 mm. lato, apice obtuso mucronatoque; perianthiis glabrescentiis.

CHINA: Shantung: Tsingtau [Tsingtao], *Zimmerman* 205 (TYPE), 448.

This variety can be distinguished by its very deeply cut lanceo-elliptic segments of the leaves which are obtuse at the apex. In general appearance it resembles *C. hexapetala* Pall. var. *smithiana* S. Y. Hu of southern Shansi, but the latter variety has a lanate perianth and villose lower leaf surfaces.

Freyn in 1895, on the basis of *F. Karo 125b* collected from Nertschinsk [Nerchinsky], described a form which he named forma *stenophylla*. According to his description, the segments of the leaves are up to 6 cm. long and only 1 mm. wide. In the Gray Herbarium of Harvard University there is a fruiting specimen, *T. Y. Cheo & L. Yen 98*, collected from Feihshien of Shantung Province, of which the segments of the leaves are 5–9 cm. long, 3 mm. wide. Flowering material of the narrow-segmented form from the latter region is awaited for its identity.

***Tinospora craveniana* sp. nov. (Pl. I, fig. 6).**

Frutex scandens, ramis striatis sulcatisque, 2–3 mm. diametro, hor-notinis hirsutis, internodiis 7–10 cm. longis; foliis tenuiter chartaceis, sagittato-ellipticis, 5.5–11.5 cm. longis, 3–5 cm. latis, basi sagittatis, interstitio inter apices auricularum 1.5–2.5 cm. longo, apice acuminatis, acumine 5–8 mm. longo, integris, praeter nervos glabris, nervis primariis 5, palmatis, nervis secundariis laxe reticulatis, utrinque prominulis, petiolo 2.5–3.5 cm. longo, hirsuto; inflorescentiis racemosis; ♂ racemis fasciculatis, pedunculis gracilibus, 15 mm. longis, hirsutis, rhachibus 4 cm. longis, bracteis lanceolatis, 1–2 mm. longis, pedicellis 12–30 mm. longis, sparse hirsutis, prophyllis 1 vel 2; floribus 3-meris, sepalis 6, glabris, extimis oblongis, 2 mm. longis, intimis lineari-oblongis, 4–5 mm. longis, 1 mm. latis, apice acutis; petalis 6, carnosius, apice suborbicularibus, basi cuneatis, 2 mm. longis; staminibus 6, 3 mm. longis, thecis oblongis, 1 mm. longis, rimis lateralibus dehiscentibus; ovario rudimentario minuto, globoso; ♀ racemis solitariis, pedunculis 4–5 cm. longis; floribus ignotis; fructibus subglobosis, 9–10 mm. diametro, endocarpiis osseis, subhemisphaericis, 7–8 mm. diametro, ventro excavatis, dorso lineis obsoletis, inconspicuis tuberculatis.

CHINA: Kiangsi: Hwang-kong shan, Y. K. Hsiung 6402 (TYPE, fruit).
Szechuan: Mt. Omei, T. T. Yü 563 (TYPE, staminate flower).

The outline of the anterior portion of the leaf of this species appears to resemble that of *T. malabarica* (Lam.) Miers., but the base of the leaf of the latter species is cordate, not sagittate. The indumentum on the nerves of the lower surface and the sagittate leaf-base of *T. craveniana* suggest relationship with *T. sagittata* (Oliver) Gagnep., but the latter species has linear-lanceolate leaves, smaller flowers with the sepals measuring only 2.5–3 mm. in length, obtuse or rounded at the apex, and sub-orbicular anthers.

This species is named in honor of Miss Mary G. Craven, who retired in January 1953 after forty-eight years of service in the Herbarium of the Arnold Arboretum of Harvard University. Her skillful handling of the specimens has established a monument to her care of the material as well as to her friendship and association with all who have done taxonomic research in this herbarium, from the days of its founder, Charles S. Sargent, up to the present.

Tinospora imbricata sp. nov. (Pl. I, fig. 2).

Tinospora capillipes sensu Chun in Sunyats. 4: 176, fig. 34. 1940. — sensu Yamamoto in Taiwania 1: 32. 1948, pro parte, non Gagnepain, 1908.

Frutex scandens, ramulis striatis, 2.5 mm. diametro, sparse hirsutis, internodiis 7–13 cm. longis; foliis chartaceis, ovato-oblongis, 12–14 cm. longis, 4–4.8 cm. latis, basi cordatis, lobis auriculatis, imbricatis, apice caudatis, acumine 2 cm. longo, supra glabris, subtus praeter nervos glabris, nervis primariis 7, palmatis, utrinque elevatis, nervis secundariis laxe reticulatis, utrinque conspicuis; petiolo 7 cm. longo, hirsutis, basi tortile; floribus ignotis; infructescentiis subracemosis, pedunculis 3.5–9.5 cm. longis, glabrescentibus, pedicellis 9–12 mm. longis, stipite ovarii 2–5 mm. longo; fructibus rubris, subglobosis, 8–9 mm. diametro, endocarpiis pergameis, 7 mm. longis, 8 mm. latis, ventro excavatis, dorso lineis obscuris, ceterum inconspicuo-rugosis.

CHINA: Kwangsi: Yao-shan, C. Wang 40521 (TYPE).

This species occurs along the streams in central Kwangsi at altitudes of about 1300 meters. Its red fruits remain on the vine in December. Gagnepain in 1908 described *T. capillipes* on the basis of Balansa's collection from Tonkin.

The type of *T. capillipes* represents a staminate plant which has pubescent sepals. I have seen no specimen of this species. Judging from Gagnepain's illustration (Fl. Gén. Indo-Chine 1: 133, fig. 14, 11. 1908), that species is characterized by its ovate leaves with sagittate bases. The basal lobes are rounded and are far apart. Chun in 1940 interpreted C. Wang 40521 as *T. capillipes* Gagn., but Wang's collection has ovate-oblong leaves with imbricate basal lobes and represents a taxon very different from Gagnepain's species. Yamamoto did not see Wang's collection. In

recording the occurrence of *T. capillipes* Gagn. in Kwangsi he simply adopted Chun's interpretation.

***Tinospora intermedia* sp. nov. (Pl. I, fig. 5).**

Frutex scandens, ramulis vetustioribus longitudinaliter rimulosis, hornotinis hirsutis; foliis chartaceis, sagittato-oblongis, raro sagittato-ovatis, 7–11 cm. longis, 3.5–4.5 cm. latis, basi sagittatis, interstitio inter apices auricularum 3.5 cm. longo, apice acuminatis, acumine 6–8 mm. longo, apiculato; inflorescentiis staminatis fasciculatis, pedunculis 2–3.5 cm. longis, bracteis ovatis, ciliatis, 1–1.5 mm. longis, pedicellis 1–1.5 cm. longis, prophyllis 1 vel 2, ovatis, apice ciliatis, cum pedunculis glabrescentibus; sepalis 6, glabris, extimis ovatis, 1–2 mm. longis, intimis oblanceolatis, 3 mm. longis, petalis 6, carnosis, suborbicularibus, apice truncatis; staminibus 6, petalis longioribus, antheris subglobosis, 0.5 mm. diametro; infructescentiis paniculatis, pedunculis 9 cm. longis, fructibus ellipsoideis, 8 mm. longis, 7 mm. diametro, apice apiculatis, endocarpiis pergameneis, ventro excavatis, dorso ceterum lineis conspicuo-tuberculatis.

CHINA: Szechuan: Mt. Omei, *C. Y. Chiao & C. S. Fan* 263; same locality, *C. L. Chow* 5777; *W. P. Fang* 16320 (TYPE, staminate flower), 17522 (TYPE, fruit); *W. K. Hu* 8803 (sterile); *T. T. Yü* 296.

The leaves of this species appear to resemble those of *T. craveniana* S. Y. Hu in size and texture, but the basal lobes of the latter species point backward and its fruit has a bony rugose endocarp, while the basal lobes of this species all point outward and the endocarp is pergameneous and conspicuously tuberculate. The fruit characters suggest relationship with *T. szechuanensis* S. Y. Hu. Occasionally a few leaves of certain specimens, such as *Chiao & Fan* 263, are short and broad, appearing sagittate-ovate. This character suggests some relationship with *T. capillipes* Gagnepain, which has pubescent sepals. On account of its resemblance to several species in different respects, it is here treated as an intermediate species.

***Tinospora szechuanensis* sp. nov. (Pl. I, fig. 1).**

Frutex scandens, ramis striatis et sulcatis, 2.5–3 mm. diametro, hornotinis hirsutis, internodiis 6–7 cm. longis; foliis subcoriaceis, integris, sagittatis, 10–13 cm. longis, 4–4.5 cm. latis, basi sagittatis, interstitiis inter apices auricularum 5.5 cm. longis, apice acuminatis, acumine 15–20 mm. longo, cuspidato, supra glabris, subtus praeter nervos glabris, nervis primariis 5, palmatis, utrinque elevatis, nervis secundariis laxe reticulatis, supra obscuris, subtus prominulis; petiolo 5.5–6 cm. longo, glabrescente; floribus ignotis; infructescentiis paniculatis, pedunculis 9 cm. longis, axibus secundariis 10–15 mm. longis, pedicellis 5–10 mm. longis, cum pedunculis hirsutis; fructibus ellipsoideis, 11 mm. longis, 7–8 mm. diametro, stigmatis subapiculatis, endocarpiis pergameneis, subellipsoideis, 8 mm. longis, 7 mm. latis, ventro excavatis, dorso lineis conspicuo-tuberculatis.

CHINA: Szechuan: Hung-ya, Wa-wu shan, *E. H. Wilson 3528* (TYPE, fruit).

This species is characterized by its subcoriaceous sagittate leaves with the auricles pointing outward, paniculate infructescence with peduncles 9 cm. long. and ellipsoid drupes with conspicuously tuberculate parchment-like endocarp. It is closely related to *T. sagittata* (Oliver) Gagnepain, but the leaves of the latter species are linear-lanceolate, sagittate, with the auricles pointing backward, the infructescences are racemose with the peduncles 4–6 cm. long; and the fruits are subspherical with bony endocarp inconspicuously tuberculate (*Pl. I, fig. 3*).

***Tinospora yunnanensis*, sp. nov.** (*Pl. I, fig. 4*).

Frutex scandens, ramulis striatis et sulcatis, vetustioribus tuberculatis, lenticellis conspicuis, orbiculatis, elevatis, hornotinis hirsutis vel glabrescentibus; foliis subcoriaceis, sagittato-ovatis, 12–14 cm. longis, 4.5–5.5 cm. latis, basi cordato-sagittatis, auriculis rotundatis, interstitia inter apices auricularum 1.5–2.5 cm. longa, apice acuminatis, acumine 11–13 mm. longo, apiculato, utrinque rugosis, praeter nervos subtus glabris, nervis primariis 7, utrinque evidentibus, reticulatis obscuris; inflorescentiis staminatis, ramis vetustis positis, racemosis, racemis solitariis vel fasciculatis, pedunculis 4–5.5 cm. longis, glabrescentibus, bracteis lanceolatis, 2 mm. longis, apice ciliatis, pedicellis 7–10 mm. longis, pilosis; sepalis 6, extimis ellipticis, 1.5 mm. longis, 0.75 mm. latis, intimis unguicularibus, 2 mm. longis, 1.5 mm. latis, glabris; petalis 6, suborbicularibus, basi cuneatis; staminibus 6, filamentis petalis subaequalibus; ovario rudimentario globoso; floribus pistillatis fructibusque ignotis.

CHINA: Yunnan: without precise locality, *H. T. Tsai 53100* (TYPE).

This species is closely related to *T. capillipes* Gagnepain, but the latter species has villose sepals, while those of this species are glabrous.

***Chimonanthus salicifolius*, sp. nov.**

Frutex, ramulis subteretis, puberulis; foliis lineari-lanceolatis, 3–9 cm. longis, 1–3 cm. latis, basi obtusis, apice obtusis vel acutis, subcoriaceis, supra glabra, paulum nitidis, subtus opacis, hirsutis, costa utrinque elevata, nervis lateralibus 5 vel 6 paribus, reticulatis; floribus solitariis, axillaribus, pedicellis brevissimis, 4 mm. longis, bracteolis imbricatis, ovatis, puberulis; perianthiis exterioribus rotundatis, puberulis, interioribus ignotis.

CHINA: Kiangsi: Hsiu-shui, *Y. K. Hsiung 5489* (TYPE).

This species is closely allied to *C. nitens* Oliver, but the latter species has glabrous ovate-elliptic leaves with a long acuminate apex.

Euonymus orgyalis W. W. Smith in Notes Bot. Gard. Edinb. 13: 161. 1921.

CHINA: Yunnan: Si-chour hsien, Faa-dooou, *K. M. Feng 12044*; same district, Ma-chia, *K. M. Feng 12502*; Mar-li-po, Huang-jin-ia, *K. M. Feng*

13067; Mengtze. *A. Henry* 11404; Ping-pien hsien, *H. T. Tsai* 55328, 55345, 60197, 60967, 61020, 61395, 61744, 61778, and 62446.

The description of this species was based on a flowering specimen collected by *A. Henry* (10661) in southeastern Yunnan at an altitude of 2100 meters. The largest leaf of that material measures only 9 cm. long and is rounded at the base. Additional material from the same general area exhibits variations in the size and shape of the leaves and in the habit of the plant. As we now know it, the larger leaves of this species measure up to 15 cm. long and 7 cm. wide and are oblong-elliptic in shape. *Tsai* 55328, also a flowering specimen, even possesses an evergreen habit. In southeastern Yunnan the plant occurs at altitudes as low as 1300 meters, in ravines, on rocky crevices, or along the streams of the mixed forest zone. It is usually a shrub 2–3 m. high but occasionally appears scandent. The green flowers appear in late May. The specimen collected in early September has very small young fruit, the one collected in mid-October has fruit reaching mature size, and that collected in November has fruit dehiscent by apical slits. The mature fruit is globose, 12 mm. in diameter, with a rough and woody pericarp.

***Craibiodendron kwangtungense*, sp. nov.**

Craibiodendron stellatum sensu Merrill in *Lingn. Sci. Jour.* 7: 319. 1931, non (Pierre) W. W. Smith 1914.

Arbor sempervirens, 10–12 m. alta, ramulis glabris, lenticellis obscuris; foliis alternis, coriaceis, olivaceo-brunneis, supra nitidis subtus opacis, ellipticis vel lanceolatis, 6–8 cm. longis, 1.8–3 cm. latis, integris, utrinque attenuatis, basi acutis vel cuneatis, apice acutis, obtusis, raro breviter acuminatis, costa supra impressa, subtus elevata, nervis lateralibus 18–22 paribus, supra evidentibus, subtus prominentibus, margine anastomosantibus, reticulatis distinctis, stipulis obsoletis, petiolo 8–10 mm. longo; inflorescentiis racemosis simplicibus, axillaribus, rhachibus 4–5 cm. longis, minute puberulis, bracteis lanceolatis, 2 mm. longis, ciliatis, deciduis; pedicellis 2–3 mm. longis, furfuraceis puberulisque, prophyllis 2, submedio instructis; calycibus cyathiformibus, 2–3 mm. diametro, sparse puberulis, lobis 5, rotundatis, ciliatis; corolla breviter campanulata, glabra; staminibus 10, inclusis, filamentis glabris, antheris basi subsaccatis, dorso muticis; ovario globoso, 1 mm. longo, 5-loculari, stylo columnari, 2 mm. longo; capsulis depresso-globosis, 14 mm. longis, 18 mm. diametro, profunde 5-angulatis, pericarpiis ligneis; seminibus in loculo quoque 12–14, subovoideis, leviter compressis, 2 mm. longis, 2 mm. latis, alis obliquis, 10 mm. longis, 8 mm. latis, rugosulo-striatis.

CHINA: Kwangtung: Ting-wu-shan, *Y. Tsiang* 792 (TYPE, flower), 1533, 1547; Kwangsi: south of Nan-ning, Seh-feng-dar shan, *R. C. Ching* 8293 (TYPE, fruit).

Craibiodendron kwangtungense is a tree 14 meters high with a trunk 30 cm. in diameter. It occurs in southwestern Kwangtung and southeastern Kwangsi at an altitude of six hundred meters. By the lanceolate leaves,

attenuated at both ends, and the glabrous corolla, it can be distinguished from *C. stellatum* (Pierre) W. W. Smith, which has oblong leaves rounded at the apex, and pubescent corolla. It is also related to *C. henryi* W. W. Smith, which has long acuminate leaves, paniculate racemes, smaller fruits which are only 8 mm. long and 10 mm. in diameter.

Craibiodendron kwangtungense var. *frutescens*, var. nov.

Frutex 2–3 m. altus, ramulis puberulis; foliis oblongo-ellipticis, 5–6 cm. longis, 2.5–3.5 cm. latis, apice obtusis vel abrupte brevi-acuminatis, racemis puberulis simplicibus, axillaribus.

CHINA: Kwangtung: Ting-wu-shan, *W. Y. Chun* 6363. Kwangsi: Shang-sze, Shap-man-tai shan, *W. T. Tsang* 22252 (TYPE).

This variety differs from the typical *C. kwangtungense* in habit, being a shrub 2–3 meters high; also it has broader leaves and more pubescent racemes.

Ligustrum subsessile, sp. nov.

Frutex, ramulis robustis, teretis, cineraceis, triannis 5 mm. diametro, longitudinaliter minute rimulosis, lenticellis orbicularibus, cicatricibus foliorum semicircularibus, elevatis, hornotinis 2–3 mm. diametro, internodiis 2–3 cm. longis, \pm striatis, in triis sparse pilosis, ceterum glabris, lenticellis conspicuis; foliis subsessilibus, integerrimis, subcoriaceis, ovato-oblongis vel oblongis vel raro suborbicularibus, utrinque rotundatis, 4–9 cm. longis, 3–4.5 cm. latis, glabris, subtus punctatis, costa supra plana, subtus leviter elevata, nervis lateralibus 4 usque 9 paribus, supra obscuris, subtus evidentibus, petiolo 1–2 mm. longo, glabro; floribus ignotis; infructescentiis paniculatis, paniculis compactis, subcylindraceis, 4–6 cm. longis, 2–4 cm. diametro, pedunculis 1.5–2 cm. longis, sparse puberulis, rhachibus subquadrangularibus, in striis sparse puberulis, axibus secundariis 5–15 mm. longis, sparse minute puberulis, pedicellis 1–2 mm. longis, glabris; sepalis persistentibus 3 mm. diametro, lobis 4, rotundatis, glabris; fructibus oblongo-subglobosis, 5–7 mm. longis, 4–6 mm. diametro.

CHINA: Kwangsi: [Hsiu-shiu], Hwang-lung shan, Nung-lung temple, *Y. K. Hsiung* 5629 (TYPE).

This species has been reported to be a common shrub in thickets along the streams of the Kwangsi-Hupeh-Hunan border. The specimen cited above was collected in late August. The fruits are still too young for the study of the seed characters. I have not been able to match it with any *Ligustrum* in our collection. The general appearance of the compact inflorescences and of some of the smaller leaves resembles that of those shown in Hooker's illustration (*Bot. Mag.* 123: *pl.* 7519. 1897) for *Ligustrum coriaceum* Carrière, a species published on the basis of cultivated plants introduced to European gardens by Robert Fortune, reportedly from Japan. But specimens from European and Japanese gardens (such as those from Hort. Vilmorin of France, the Royal Botanic Gardens at Kew in Eng-

land, and the Botanical Garden of Tokyo) which match Carrière's and Hooker's descriptions and illustrations, all have smaller leaves, the smallest ones being 1.5 cm. long, 1 cm. wide, and the largest ones being 4 cm. long, 3 cm. wide. They all have comparatively longer petioles which are 3-7 mm. long. In comparing them with Hsiung's collection from Kiangsi, I conclude that the latter, with its sessile large leaves, is specifically distinct.

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EXPLANATION OF THE PLATES

PLATE I

FIG. 1. A habit sketch of a fruiting branch of *Tinospora szechuanensis* showing the basal lobes of the leaf pointing outward. FIG. 2. A habit sketch of a fruiting branch of *Tinospora imbricata* showing the imbricate basal lobes of the leaf. FIG. 3. A habit sketch of a staminate flowering branch of *Tinospora henryi* with a separate flower enlarged 5 times. FIG. 4. A habit sketch of a leafy branch of *Tinospora yunnanensis* and a staminate flowering branch showing the inflorescences on old growth, with a separate staminate flower and a smaller outer and a larger inner sepal enlarged 5 times. FIG. 5. A habit sketch of a fruiting branch of *Tinospora intermedia* with a separate staminate flower enlarged 5 times. FIG. 6. A habit sketch of a fruiting branch of *Tinospora craveniana* with a separate staminate flower enlarged 5 times.

PLATE II

FIG. 1. A habit sketch of *Craibiodendron kwangtungense* showing solitary axillary racemes. FIG. 2. A flower after anthesis ($\times 10$). FIG. 3. Two anthers, dorsal and sublateral view ($\times 18$). FIG. 4. A fruit ($\times 1\frac{1}{2}$). FIG. 5. A seed ($\times 5$).



SPECIES OF TINOSPORA



CRAIBIODENDRON KWANGTUNGENSE HU

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